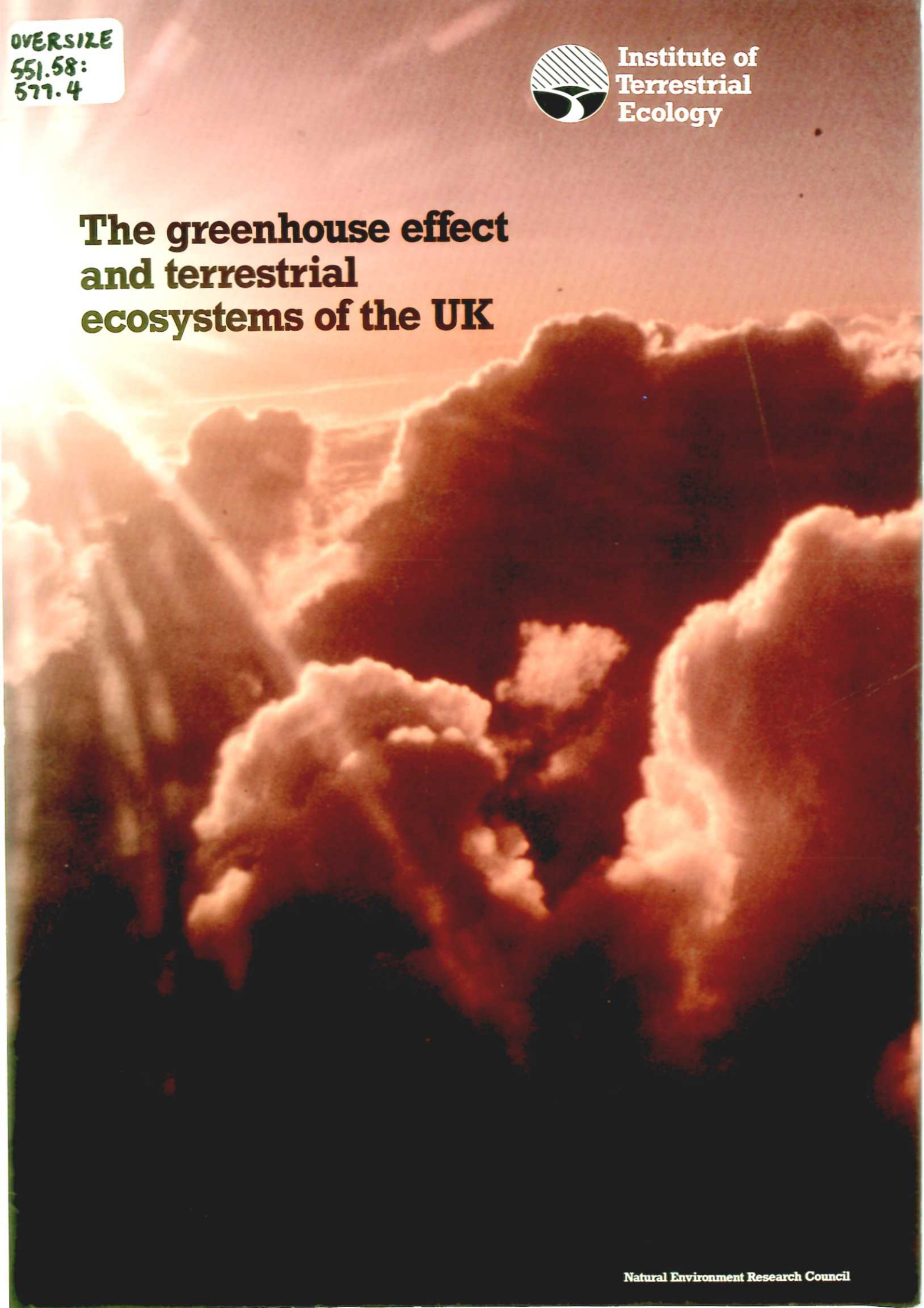
Institute of Terrestrial Ecology

The greenhouse effect and terrestrial ecosystems of the UK



Natural Environment Research Council

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The greenhouse effect and terrestrial ecosystems of the UK

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The INSTITUTE OF TERRESTRIAL ECOLOGY (ITE) is a component research organisation within the NATURAL ENVIRONMENT RESEARCH COUNCIL. The Institute is part of the Terrestrial and Freshwater Sciences Directorate, and was established in 1973 by the merger of the research stations of the Nature Conservancy with the Institute of Tree Biology. It has been at the forefront of ecological research ever since. The six research stations of the Institute provide a ready access to sites and to environmental and ecological problems in any part of Britain. In addition to the broad environmental knowledge and experience expected of the modern ecologist, each station has a range of special expertise and facilities. Thus, the Institute is able to provide unparallelled opportunities for long-term, multidisciplinary studies of complex environmental and ecological problems.

ITE undertakes specialist ecological research on subjects ranging from micro-organisms to trees and mammals, from coastal habitats to uplands, from derelict land to air pollution. Understanding the ecology of different species of natural and man-made communities plays an increasingly important role in areas such as monitoring the ecological aspects of agriculture, improving productivity in forestry, rehabilitating disturbed sites, assessing the causes and effects of pollution, managing and conserving wildlife, and controlling pests.

The Institute's research is financed by the UK Government through the science budget, and by private and public sector customers who commission or sponsor specific research programmes. ITE's expertise is also widely used by international organisations in overseas collaborative projects.

The results of ITE research are available to those responsible for the protection, management and wise use of natural resources, being published in a wide range of scientific journals, and in an ITE series of publications. The Annual Report contains more general information.

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Foreword

The Institute of Terrestrial Ecology has long been at the forefront of studies to determine the effect of environmental factors on community processes in natural and semi-natural ecosystems. The Institute has built up numerous long-term data sets which will form the basis for quantifying some of the effects of recent global warming. These analyses will be an essential prelude to formulating experimental investigations and developing predictive models of changes in ecosystem function and species distribution.

The Institute has considerable experience in studies of the processes which control carbon balances and trace gas fluxes in terrestrial ecosystems. There will be increasing opportunities for linking these local studies to remotely sensed parameters of ecosystem structure and function in order to extrapolate the information to the regional and global scale.

The Directors wish to express their appreciation to the authors and to the editors of this volume, who have combined a range of presentations into a format which provides an indication of the wide range of data and expertise available in the Institute. The challenge is to integrate the Institute's capabilities with universities and other institutes to develop an international programme predicting the consequences of increased CO_2 emissions and global climatic change.

O W Heal and T M Roberts

Preface

A few years ago, the notion that man could warm the earth by producing greenhouse gases was treated with some scepticism, despite the considered opinion of many scientists over nearly 20 years and the CO_2 record from Mauna Loa. Today, almost everybody is familiar with the notion, and most scientists accept that some warming will probably occur. Of course, it is uncertain how much warmer the earth will be, how regional climates will be affected, and how soon an effect will be observed, but these uncertainties are no reason to ignore the probability. By the time we are certain, it will be too late to stop considerable further warming, and we shall have to respond all the faster to the impacts. It is better to consider the likely impacts now and to develop the knowledge that might be needed in 20–30 years' time. It is also necessary to consider action that can mitigate or exploit potential effects.

It was with this background in mind that the Institute brought together ideas from a wide range of disciplines on the likely ecological impacts of climatic warming in the UK. In some instances, the general relationships between climate and an organism or ecosystem are well known, but, in many instances, we are left with clues, guesses and questions which form hypotheses for further research.

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1. Carbon dioxide and the global carbon cycle

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1.1 Introduction

The purpose of this chapter is to outline the current state of knowledge concerning the principal greenhouse gas, carbon dioxide. What is its role in the earth's energy balance? How are levels of CO_2 rising in the atmosphere? What is the exchange of atmospheric CO_2 with the ocean and land surfaces? How much CO_2 is being emitted? What are the projections for the future?

1.2 CO_2 and the greenhouse effect

Carbon dioxide is the main gas present in the atmosphere which is transparent to incoming short-wave solar radiation but absorbs outgoing infra-red radiation. The other gases with similar properties are methane, nitrous oxide, ozone and certain chlorofluorocarbons (CFCs) (see Chapter 2).

Imagine that 100 units of solar radiation strike the top of the atmosphere, as shown in Figure 1. Some units are reflected back into space, but about 23 units are used to heat up the atmosphere and about 46 units heat up the earth's surface. The warm surface of the earth (275–300°K) then radiates 115 infra-red units (106+9) towards the atmosphere, of which 106 are absorbed by the atmosphere. The atmosphere, in turn, radiates 60 units out into space. The difference, 106−60=46 units, is caused by gases such as CO_2. This is the greenhouse effect. Without this effect, the earth would be about 33°C colder than at present. What we are concerned with is a small enhancement of this effect.

Figure 2 shows the energy in the infra-red spectral bands that are radiated from the earth's surface. The greenhouse gases absorb radiation within these spectral bands; CO_2 and ozone can be seen to produce noticeable 'holes' in the emission spectrum. Molecule-for-molecule, methane, nitrous oxide, ozone, and especially CFCs, are more effective absorbers of infra-red radiation than CO_2. However, CO_2 occurs at much higher concentrations than the other greenhouse gases, and currently contributes about half of the greenhouse effect (McElroy 1988).

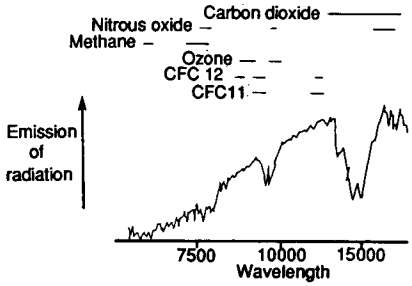

Figure 2. The energy emitted by the earth in different wavelengths, showing the wavelengths absorbed by the principal greenhouse gases

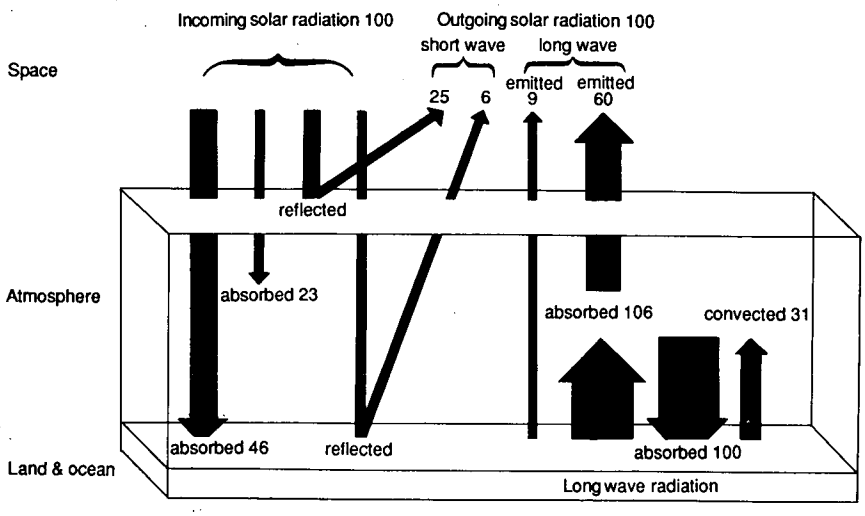

Figure 1. The earth's energy budget, scaled to 100 incoming and 100 outgoing arbitrary units of solar radiation

Fluctuations in levels of atmospheric CO_2 over past centuries have been measured in bubbles trapped in ice cores, eg the Vostok core (Barnola *et al.* 1987). Over a period of 160 000 years, fluctuations over the range 200–300 ppmv (parts per million by volume) seem to have been associated with fluctuations in the earth's temperature (deduced from concentrations of isotopic oxygen and ice extents) – high CO_2 levels have been associated with high temperatures.

1.3 CO_2 levels in the atmosphere

Ice core data show that, in the middle of the last century, before the industrial revolution, the concentration of CO_2 in the atmosphere was 275 ± 10 ppmv (Neftel *et al.* 1985). Data collected at Hawaii's Mauna Loa Observatory show an indisputable increase from 315 ppmv in 1958 to 350 ppmv in 1988 (Figure 3). CO_2 concentrations are still rising, and are now higher than at any time over the last 160 000 years (Barnola *et al.* 1987). Other evidence of increasing CO_2 levels comes from increases in the partial pressure of CO_2 in the surface waters of the oceans (Reichle, Trabalka & Solomon 1985) and from decreases in the amounts of ^{14}C in tree rings since about 1850 (Bolin 1986).

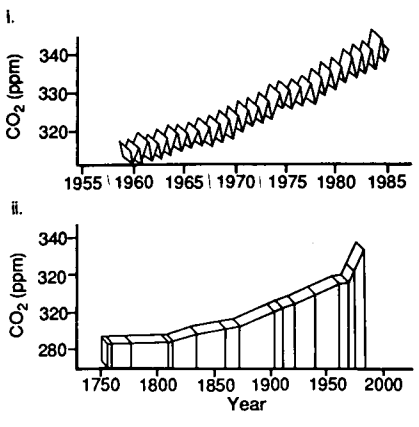

Figure 3. Increases in atmospheric CO_2 levels recorded in the air at (i) Mauna Loa, and (ii) in ice bubbles

CO_2 is generally well mixed in the atmosphere, with mean annual differences of only 1–2 ppmv between high northerly and southerly latitudes (Bolin 1986). However, at northerly latitudes, the concentration fluctuates seasonally by about 12 ppmv – being higher in winter, while at southerly latitudes the annual fluctuation is only about 2 ppmv. This seasonal fluctuation is due principally to summer-time photosynthesis, especially by northern forests. Recently, it has been shown that the annual amplitude of CO_2 concentrations is increasing, with more rapid draw-down rates in spring, possibly reflecting faster CO_2 fixation by northern forests in response to CO_2 fertilisation itself (D'Arrigo, Jacoby & Fung 1987).

1.4 The global carbon cycle

Atmospheric CO_2 levels are rising because carbon locked up in fossil fuels and tropical forests is being released by burning or decomposition. However, only about half of the CO_2 released remains in the atmosphere. To understand what is happening, we need to examine the global carbon cycle (Figure 4).

There are four important reservoirs of carbon in the world:

oceans ($37\,000 \times 10^{15}$ g C, or 37 000 gigatons) where carbon exists mainly as carbonates;

organic matter in soils and litter ($1300–1400 \times 10^{15}$ g C);

atmospheric CO_2 (725×10^{15} g C);

plant biomass (560×10^{15} g C) where carbon comprises about half of the dry matter.

In addition, there are fossil fuel reserves (coal, oil and gas) of $5000–10\,000 \times 10^{15}$ g C.

Currently, about 5×10^{15} g C is being released into the atmosphere each year by burning fossil fuels, and, arguably, another 1×10^{15} g C is being released each year by deforestation (including the breakdown of soil organic matter).

In the absence of deforestation, the carbon budget between the land and the atmosphere would approximately balance; about 120×10^{15} g C is fixed by photosynthesis each year, half of which is returned to the atmosphere by respiration, and half of which is eventually returned by microbial decay (respiration) in the litter and soil.

The major sink for atmospheric CO_2 is the ocean, which absorbs about 93×10^{15} g C annually, but releases only 90×10^{15} g C, thereby absorbing 3×10^{15} g C, half of the 6×10^{15} g C emitted annually by fossil fuel burning and deforestation. Thus, only about 50% (probably less, Bolin 1986) of the CO_2 emitted by man's activities remains in the atmosphere.

The simple picture presented so far hides enormous complexity and ignores considerable uncertainty about the magnitude of the carbon fluxes. Consider, first of all, carbon uptake by the oceans. There are physical processes of dissolution, and biological processes of CO_2 fixation by phytoplankton. The solubility of CO_2 increases with decreasing

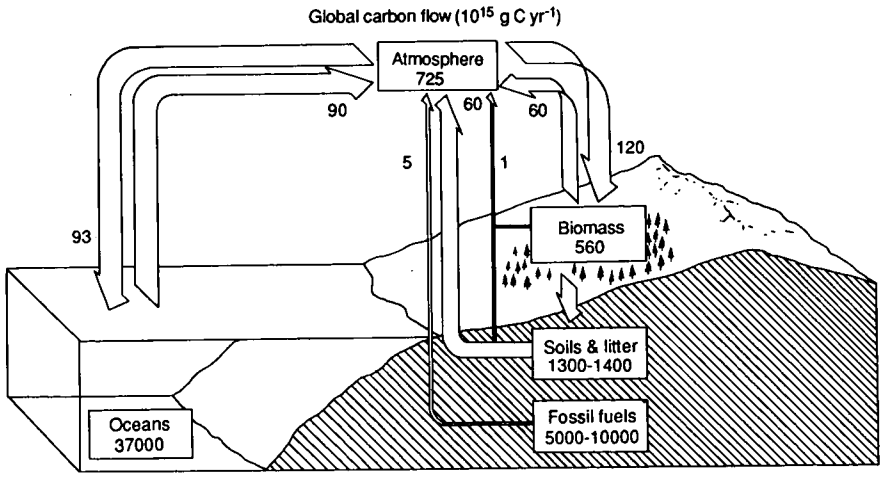

Figure 4. A simple global carbon budget. Note that most of the numbers given here are known only approximately

temperature, so high-latitude oceans are sinks, whereas tropical oceans can be sources, and so ocean circulation patterns become important. The physical uptake of CO_2 also depends on the amount of dissolved inorganic carbon (DIC) in the surface waters (the buffering capacity): as more DIC accumulates, CO_2 becomes less soluble. In fact, the concentration of DIC is much lower in surface waters than at depth; if it were not, and the oceans were well mixed vertically, then surface DIC levels would be about 15% greater than now and atmospheric CO_2 levels would be about 700 ppmv. Clearly, ocean upwelling processes are important. Perhaps more important is phytoplankton photosynthesis, which removes CO_2 from the surface waters and fixes it in dead organic matter or carbonate shells that fall to the bottom. A small increase in net photosynthesis of phytoplankton of, say, 1% would decrease atmospheric CO_2 levels by 2–7 ppmv (Bolin 1986). Such an increase could occur, for instance, as a result of ocean warming, a greater nutrient supply from the land or upwelling, or from CO_2 fertilisation itself.

The terrestrial carbon cycle is also complex. Photosynthetic rates vary for different vegetation, and the carbon remains in different compartments of the biomass and soil for different periods before being released. Thus, carbon put into leaves is released within months, whereas carbon that finds its way into the stable humus in soils can stay there for hundreds of years. The situation is greatly complicated by man's interference in the natural carbon cycle by altering land uses (deforestation, afforestation, etc), forming charcoal, acidifying soils, altering nutrient supplies (including atmospheric pollutants), and by CO_2 fertilisation itself (which may increase the amount of carbon stored in vegetation globally). Estimates of the net emission of carbon from the land surface vary from 0.5 to 2.5×10^{15} g C per year.

Thus, the exact amount of CO_2 emitted from the terrestrial biosphere is unknown; the exact magnitude of the land and ocean sources and sinks are unknown; and it is uncertain whether 50% of future net emissions of CO_2 will continue to be absorbed by the oceans and other natural processes when greenhouse warming occurs.

1.5 Emissions of CO_2 and future projections

Notwithstanding the uncertainties regarding the fate of CO_2 in the global carbon cycle, the major uncertainty about future atmospheric CO_2 levels is the amount that will be released by burning fossil fuels, and, to a lesser extent, by changing land uses. Given that the total amount of carbon contained in the world's forests is around 200×10^{15} g C, and that the peak period of world deforestation has probably passed (Peng *et al.* 1983), it seems unlikely that future emissions from the forests and soils will exceed $1–2\times 10^{15}$ g C per year. By contrast, fossil fuel reserves contain $5000–10\,000\times 10^{15}$ g C, and it is conceivable that annual emissions could rise from 5 to 20×10^{15} g C, or fall to 2 or 3×10^{15} g C (Keepin, Mintzer & Kristoferson 1986). There is enough fossil fuel available to increase atmospheric CO_2 levels to 1000 ppmv, making any reasonable assumptions about the global carbon cycle.

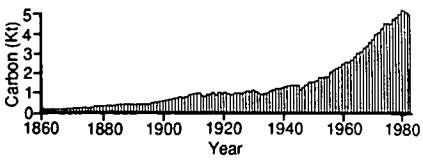

Figure 5. Annual global emissions of carbon from fossil fuels since 1860

The release of CO_2 by burning fossil fuels increased rapidly after about 1950 (Figure 5), and the percentage of the world's emissions emitted by different nations has shifted dramatically, so that China, Japan and India are now major CO_2 sources (Figure 6).

A number of complex, inter-related factors make it impossible to forecast global CO_2 emissions from fossil fuels in the 21st century. The most detailed studies have a two-fold variation, looking ahead no further than 2000 AD (Keepin *et al.* 1986).

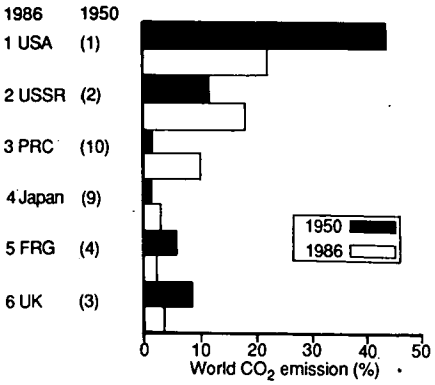

Figure 6. Change between 1950 and 1986 in the percentage of the world's CO_2 emitted by six nations

First, fuels differ in the amount of carbon emitted per unit of energy released: gas is the cleanest fuel and coal is the dirtiest, while nuclear fuels, of course, emit no carbon (Figure 7). Thus, scenarios based on nuclear fuel or an increased reliance on natural gas (methane) give slow rates of increase in atmospheric CO_2 (eg Ausubel, Grübel & Nakicenovic 1988).

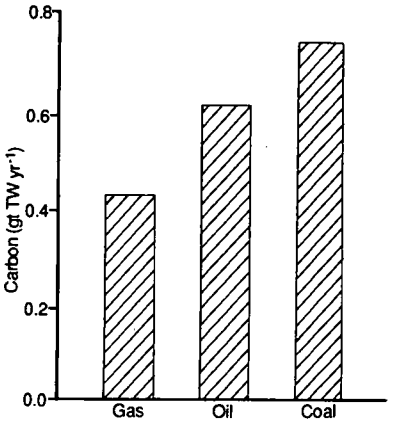

Figure 7. Amount of carbon emitted per terrawatt of energy released from different fossil fuels

Second, the carbon emitted by nations (ie the amount of fuel they burn) is not closely coupled to their economic output (Figure 8). There are great differences in energy use efficiency – in the insulation of buildings, in industrial processes, and in automobile design. Developing economies tend to be the least energy-efficient. However, the USA could reduce its CO_2 emissions by 25% by being more energy-efficient, thereby cutting global CO_2 emissions by about 7%. In the UK, about half of our CO_2 is emitted in

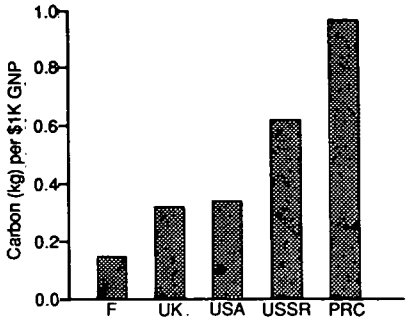

Figure 8. Amount of carbon emitted per dollar of economic output by different nations

order to supply buildings with heat and electrical energy, and great savings could be made by improving insulation and the efficiency of appliances. International efforts to transfer and improve technologies to use energy efficiently would benefit all parties.

Third, and most uncertain of all, is the future of world economic policies, international relations, energy cartels, technical developments, and so on. Nobody could have foreseen the 1973–74 oil crisis, or the recent events in the People's Republic of China and in eastern Europe.

Consequently, forecasts of future atmospheric CO_2 levels vary widely (Figure 9). At the upper limit, pre-industrial levels of 275 ppmv will double to 550 ppmv by about 2030, whereas, at the lower limit, concentrations may never exceed 400 ppmv. The 'best guess' is that doubling will occur towards the end of the next century.

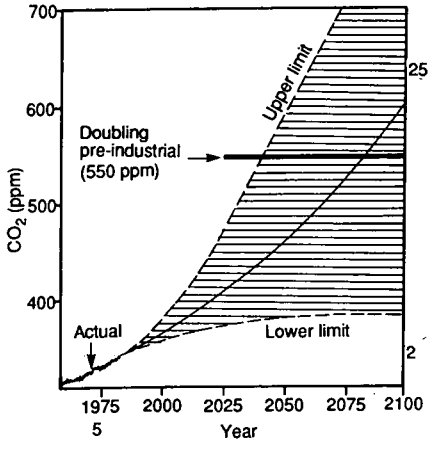

Figure 9. Upper and lower limits of projected atmospheric CO_2 concentrations

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THE GREENHOUSE GASES

2. Methane, ozone, nitrous oxide and chlorofluoro-carbons

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2.1 Introduction

The principal radiative effect of the greenhouse gases is to absorb parts of the long wavelength (infra-red) radiation emitted by the earth's surface and the atmosphere. The combined effect of these gases leads to a global average surface temperature of 283°K, rather than the much cooler 253°K surface temperature for the earth with no atmosphere.

The key greenhouse gas species (excepting water vapour whose global average concentration is not believed to be changing, and CO_2 which is considered in the previous Chapter) are methane (CH_4), nitrous oxide (N_2O), ozone (O_3), and several of the chlorofluorocarbons, notably F11 ($CFCl_3$) and F12 (CF_2Cl_2). The radiative properties of each of these trace gases differ considerably, although they all have important absorption bands in the 7–15 μm thermal radiation wavelengths (see Chapter 1).

The relative importance of each of the trace gases in the radiative budget can be illustrated by their individual effect on average global surface temperature following an assumed doubling of present concentrations (Table 1). Taken together, the potential for changes in surface temperature resulting from a doubling in concentrations is of a similar order (2–4°C) to the surface temperature response to a doubling of CO_2 concentration. While it is unlikely that all of the trace gases, including CO_2, will increase at the same rate, it is clear that large and important changes are taking place in the concentrations of *all* these species (methane, nitrous oxide, ozone and the chlorofluorocarbons F11 and F12).

The increase in CO_2 concentration has been monitored and documented in considerable detail during the last 20 years, so that, while uncertainties in the global cycle of carbon remain, the basic processes are much better understood than those for the other trace gases. The following sections briefly outline the sources and sinks for methane, ozone, nitrous oxide and CFCs.

2.2 Methane

The current atmospheric concentration of methane is about 1.7 ppmv and is increasing at almost 2% per year. The surface temperature would increase by about 1°K for a doubling of the current methane concentration assuming only the direct radiative effects. In practice, the atmospheric chemistry of methane in the background troposphere is closely coupled with that of other trace gases. By competing with carbon monoxide and with ozone for reaction with hydroxyl (OH) radicals, methane may influence the concentrations and the atmospheric lifetimes of other trace gases which are also important in the radiative budget of the atmosphere.

The atmospheric residence time of methane is about 10 years and is long relative to the very reactive trace gases in the atmosphere (eg ozone at 0.01 yr). The principal sink for loss of methane from the atmosphere is reaction with OH radicals in the troposphere (80%) and stratosphere (10%). The remaining 10% is removed at the ground by methane-consuming aerobic micro-organisms.

Table 1. Effect on global temperatures (at equilibrium) of doubling the present nominal concentration of the main greenhouse gases

	Nominal concentration (ppbv)[1]	Temperature increase (°C)
CH_4	1700	0.95
N_2O	320	0.25
O_3 total	*	2.0
O_3 troposphere	*	1.1
CF_2Cl_2 (F12)	0.2	0.1
$CFCl_3$ (F11)	0.1	0.03

[1] Parts per billion by volume

* The concentration of ozone varies with altitude in both the troposphere and in the stratosphere

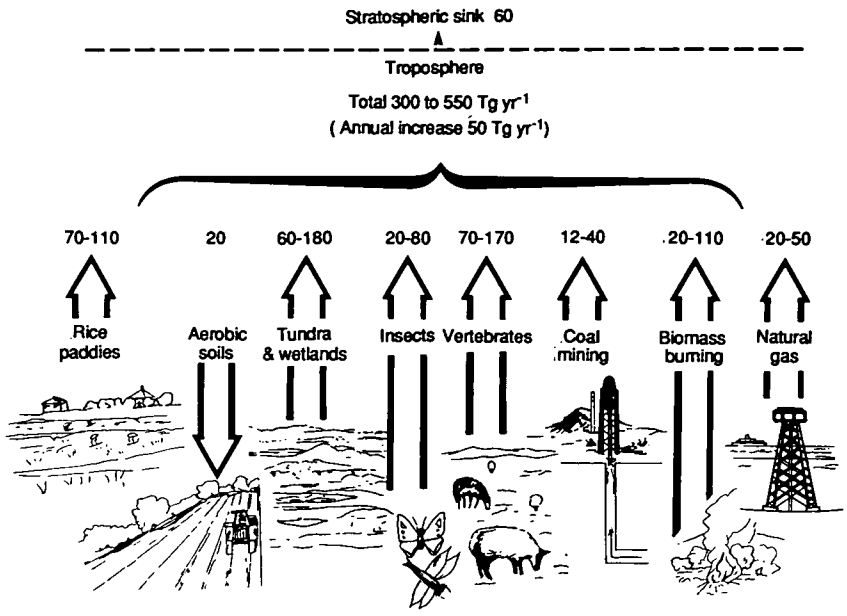

Figure 1. A possible global budget for methane (all values in Tg yr^{-1})

A knowledge of the atmospheric chemistry of methane has been used so far to deduce average removal rates from the atmosphere of about 400 Tg per year. Although there is uncertainty about at least 20% of this estimate, it is generally believed to be much better known than the source terms, so that the overall budget is constrained by the rate of increase in concentration and the chemical removal.

Sources

The sources of methane include rice paddies, wetland and tundra, insects, the digestive tracts of ruminants, coal mining, biomass burning, and the leakage of natural gas (Figure 1).

The total input to the atmosphere lies in the range 300–550 Tg per year. Of the sources, only one is well understood and well estimated, and this is enteric fermentation in mammals (mainly ruminants), which results in a flux to the atmosphere of 85 (±15) Tg per year. The two sources generally regarded as the dominant terms are methane production by anaerobic fermentation of organic material by bacteria in rice paddies and in the northern wetlands. Of these two sources, the methane released from rice paddies may be expected to have increased in proportion to the area of rice grown, and hence to the rise in population (Figure 2).

The increases in methane concentration over the last 600 years are derived from air samples which have been extracted from dated ice cores from Greenland and Antarctica. These samples provide the most conclusive evidence to date of the changes in concentrations of relatively unreactive trace gases (those with residence times in the atmosphere greater than one year). Data from the Vostok ice core in Antarctica extend back through the last glacial-interglacial cycle (160 000 years), and the rise and fall in global temperatures and methane are strongly correlated.

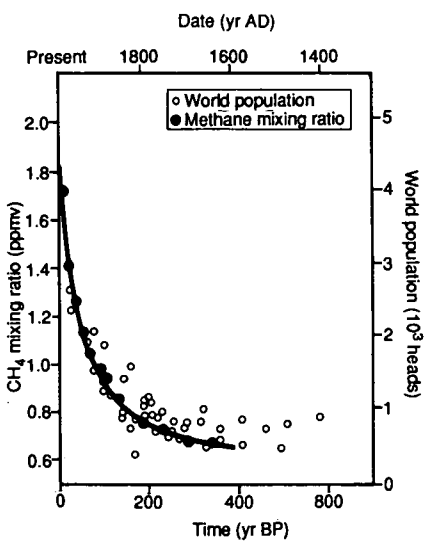

Figure 2. The increase in atmospheric levels of methane over the last 600 years compared with the increase in world population. Methane values were measured in air bubbles in the Greenland ice sheet

The cause of the strong link between global temperature and methane may be either atmospheric (through its radiative properties) or source-related. We do not have sufficient information to know whether methane production from the northern wetlands is changing, but recent work suggests that a significant fraction of the observed methane increase *could* have been caused by warming at high latitudes. There could be a large increase in methane emission in response to small warming in these regions.

In the UK, there is a significant wetland area (about 7% of the land area) from which methane release has been measured at about 10 mg C m^{-2} day^{-1} (about 6000 tonnes C to the atmosphere annually for the UK). Similarly, fluxes of methane from landfill sites have recently been measured, and over the next decade the measurement of all major land sources is planned. However, it is naive to consider methane on a national scale, except for comparison with the global picture, because methane's long residence time (about 10 years) leads to a rather uniform global methane concentration.

The global budget for methane is summarised in Figure 1. Included in this budget is an estimate of the uncertainty in individual values which are the upper and lower boundaries of published estimates. The best and reasonably well-known components are the losses by chemical reaction in the troposphere and the stratosphere and the vertebrate emissions. The emissions from rice paddies are much less variable in recent publications, with values close to 100 Tg per year; insect (notably termite) emission estimates appear to be much smaller than earlier estimates (Ehhalt 1988). However, the remaining uncertainty provides considerable scope for revision. In particular, biomass burning and wetland emission estimates are based on very few measurements.

2.3 Ozone

Most atmospheric ozone is present in the stratosphere, which, in addition to its important absorption of short wavelength solar radiation, also absorbs at the thermal wavelength. Important changes in stratospheric ozone concentration have been observed over the Antarctic (Farman, Gardiner & Shanklin 1985), with concentrations in the Antarctic spring 50% smaller than they were ten years ago. Changes in global stratospheric ozone are much less clear. There is evidence of a decrease in stratospheric ozone of 2–3% during the last decade, but about half of this change may be attributed to changes in solar activity. The causes of the remaining change remain uncertain.

Concentrations of ozone in the troposphere are much smaller than those in the stratosphere, and account for only 10% of the total ozone. The lifetime of ozone in the troposphere is short (a few weeks), and the different source and sink strengths of different regions of the world therefore lead to substantial spatial variability in ozone concentrations. This spatial variability makes it difficult to extrapolate local trends in concentrations to global scales. However, there is evidence that tropospheric ozone concentrations in Europe and North America have increased substantially during the last few decades, possibly by a factor of two (Penkett 1988).

Sources and sinks

Unlike the other radiatively active trace gases, ozone has an important sink at the ground by dry deposition. The sources of ozone in the troposphere include transfer from the stratosphere, and photochemical ozone production within the troposphere. The production of ozone in the troposphere results from the photolysis of nitrogen dioxide.

$NO_2 \longrightarrow NO+O$ (for wavelengths <400 nm)

$O+M+O_2 \rightarrow O_3+M$

The ozone produced may react with nitric oxide to form NO_2, and a photostationary state is established. This equilibrium may be disturbed by a range of other gases, including peroxy radicals and involving CO and CH_4. In practice, this leads to net ozone production whenever $NO_x(NO+NO_2)$ exceeds 30 pptv (parts in 10^{12}). NO_2 concentrations have been shown to exceed this threshold across large areas of the northern hemisphere as a result of emissions from industry, vehicles and farmland. Thus, a substantial fraction of the tropospheric ozone currently observed in the northern hemisphere may well be a result of anthropogenic activity.

2.4 Nitrous oxide

The trend in global nitrous oxide concentrations is upwards, but at a lower rate than methane, about 0.3% per year (Figure 3). The current average concentration is about 318 ppbv. Ice core analyses, similar to those for methane, have demonstrated the marked recent increase from about 290 ppbv during the last century to the current value, the increase being confined largely to the last 40 years. There were no large concentration changes in the pre-industrial period extending back 3000 years.

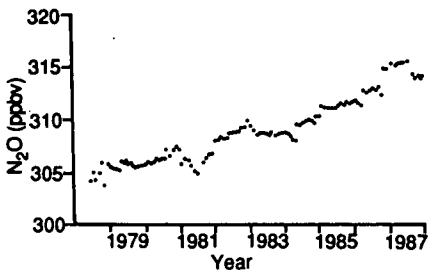

Figure 3. The increase in atmospheric levels of nitrous oxide (N_2O) measured in the surface air at the Cape Grim Observatory, Tasmania

Unlike methane, nitrous oxide has no significant sink in the troposphere. It is a rather unreactive gas, and does not undergo chemical reaction with the ground, vegetation or any of the tropospheric constituents. Nitrous oxide is removed by photolysis and by reaction with excited oxygen atoms in the stratosphere, which then leads to ozone destruction through the catalytic cycle:

$NO+O_3 \rightarrow NO_2+O_2$

$NO_2+O \rightarrow NO+O_2$

the net result being $O_3+O \rightarrow 2O_2$.

The stratospheric chemistry sink for nitrous oxide has been estimated to remove between 6 and 10 Tg N_2O per year (Crutzen 1979). This sink strength, with a total content of nitrous oxide in the atmosphere of 1.5 Gt (as nitrogen), implies a residence time of about 170 years. To balance the sink term and the observed increase of 3–5 Tg yr^{-1} requires a source in the range 9–15 Tg yr^{-1}.

Sources

The pre-industrial amount of nitrous oxide at 280 ppbv must have been in equilibrium with the sources (because concentrations were constant over long periods). The natural sources must, therefore, have been between 5 and 9 Tg per year.

The current emissions represent a substantial increase over the earlier values. The sources of nitrous oxide include denitrification (and nitrification) in soils, and are stimulated by applications of mineral fertilisers. The global loss of nitrogen as nitrous oxide from fertilisers has been estimated to be in the range of 1–4% of the applied fertiliser, with an annual average of 1.5 Tg. Nitrous oxide is also formed by nitrification in ocean water and is emitted into the atmosphere, possibly at the rate of 2 Tg yr^{-1}. The combustion of fossil fuel and wood also releases nitrous oxide into the atmosphere; various authors have suggested that this may be a major source, but recent analyses imply values between 1 and 2 Tg yr^{-1}. Lightning has also been proposed as a major source, but the consensus is that this contribution could not be more than 0.1 Tg yr^{-1} to the global budget.

Clearly, the uncertainties in the global budget for nitrous oxide are large, and the construction of a global cycle in which known sources are summed and compared with sinks is speculative (Figure 4). The budget can be made to match sources and sinks because of the large uncertainties among the components, but a wide range of further field and laboratory studies will be necessary to reduce the scale of these uncertainties.

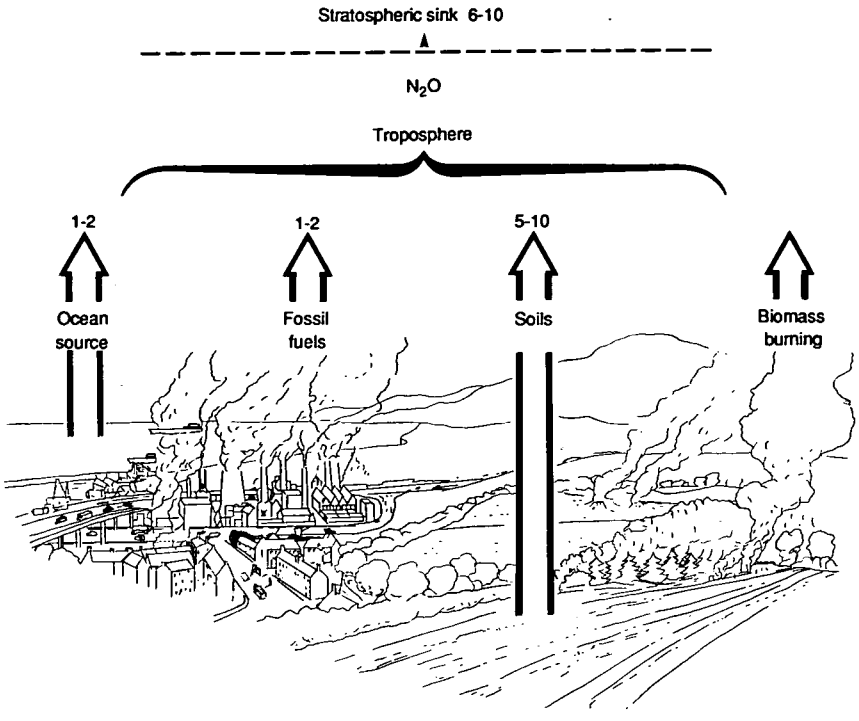

Figure 4. A possible global budget for nitrous oxide (all values in Tg yr^{-1})

2.5 Chlorofluorocarbons

The CFCs are produced for a range of applications, such as refrigerants, spray can propellants and solvents. The most common CFCs, and the two most important for global climate change, are $CFCl_3$ (also known as F11) and CF_2Cl_2 (F12).

There are no natural sources of F11 and F12 chlorofluorocarbons. Their presence in the atmosphere has been known since the 1970s, when the possibilities of ozone removal by chlorine from CFCs and the contributions of CFCs to global warming were identified.

The rate of increase of CFCs is large, at about 5% per year, and their atmospheric residence times have been estimated at 80 years for F11 and 170 years for F12. These long residence times imply that it will take many years to recover from the effects of CFCs, even if the 1988 Montreal Protocol (which does not apply globally) is fully upheld.

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3. Soil processes

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3.1 Introduction

It is comparatively easy to accept the concept that most species of plants and animals are strongly affected by climate; it only takes a few abnormal weather patterns to reveal the narrow climatic bands to which a large number of plants, and their pests, are restricted. Much less obvious, yet of equal importance, are the processes occurring beneath our feet, namely those occurring in the soil. Soils are both affected by, and contribute to, climatic change.

Soil is the product of physical and chemical processes working on rock, causing disintegration and decomposition, and resulting in a varied and complex substrate, essential for all terrestrial life. The most obvious, and very important, part of the soil is the surface layer, where the majority of biological activity and input of organic matter occurs. Beneath this surface, or A horizon, is a second layer where some of the materials migrating from the A horizon tend to accumulate, referred to as the B horizon. The A horizon is called the eluvial (washing out) zone, and the B horizon the illuvial (washing in) zone. The soil's parent material sits beneath these and is referred to as the C horizon.

The structure of the soil results from the interaction between climate and the parent material, on to which the influences of management are superimposed. Climate exerts a major effect on soil formation through such processes as frost/thaw cycles and the occurrence of rainfall of varying intensity and frequency. Additionally, climate determines the type of vegetation that develops, particularly in natural ecosystems, and the vegetation types can markedly affect soil formation through organic matter inputs, root activity and transpiration. There are strong links between soil type and climatic zone in the UK, but the correlations are often secondary and associated with altitudinal effects.

Soils are important sources of several gases associated with climatic change, namely carbon dioxide (CO_2), methane (CH_4) and oxides of nitrogen (N_2O and NO_x). Thus, soils are not only likely to be affected by climatic change, but also contribute to it, and recent estimates of these contributions are discussed in Chapter 2 and referred to below.

3.2 Impact of climatic change on soils

The vertical arrangement of the soil horizons is referred to as the soil profile, and numerous variations in this basic arrangement exist, dependent upon local conditions, climate, topography and the nature of the parent material. The formation of these horizons is a dynamic process, and is very strongly governed by climate. Soils are classified on the basis of the presence or absence of the horizons, their composition within specified depths, and the hydrological conditions governing their development. Based on the structure of the upper 1.5 m, the Soil Survey of England and Wales (Avery 1980) recognises ten major soil groups in the UK, with more than 100 soil subgroups.

The importance of vegetation in the processes of soil formation is perhaps most apparent in the A horizon, where plant materials are added to the soil and the rate of decomposition is greatest. During the process of decomposition, organic matter is transformed by soil fauna and microflora both to fundamental constituents and to more slowly decomposing humus. The fundamental constituents range from carbon dioxide gas to mineral nutrients, such as calcium, nitrogen, potassium and phosphate. In base-rich, well-aerated soils, the pH is usually high, and the process of decomposition is usually rapid, often helped by the macrofauna, such as earthworms. The macrofauna also mix the soil, facilitating nutrient release and the mixing of minerals and organic matter.

In soils deficient in bases, the soil fauna are usually smaller in size, and are unable to mix the soil. Thus, acid soils are often characterised by accumulations of surface organic matter, and the formation of deep peats occurs because low summer temperatures, waterlogging and soil acidity inhibit decomposition to such an extent that it is almost halted. High

rainfall causes leaching from the soil of any bases remaining, so that the soil becomes increasingly acidic. A comparison of the distribution of rainfall in the UK with the occurrence of peat soils shows a close correlation.

Figure 1 shows the general relationship between soils, climate and relief, providing some indication of the interactions between soils and climate. However, it must be emphasised that a simple comparison of soils formed under different climates does not necessarily indicate the changes that will occur when a soil formed under one climatic regime is subjected to a second climatic regime. Thus, the simplistic assumption that marginal upland peat soils formed on gentle slopes will revert to stagnohumic gleys as the climate becomes warmer and drier is invalid, because the decomposition of organic matter accumulated in the peat will cause other changes in the lower soil horizons. Similarly, soils which have been subjected to high rainfall will have had most of the bases leached from the soil over the centuries, and a reduction in contemporary rainfall or increased evaporation will do nothing to replace those bases. Some of the interactions described will result in soils developing in ways which have not previously been observed.

It is an onerous, if not impossible, task to predict the implications of every permutation of climatic change on soil processes, and one has to start by assuming that climatic changes will occur in certain directions and within certain limits. For the current purposes, it will be assumed that temperatures will rise in the UK over the next 50 years by the order of 3°C, and that rainfall will either increase or decrease by 10%.

Changes in climate will result in a variety of changes in soil processes, including effects on hydrological pathways, decomposition processes and mineral weathering. The responses will vary between soils, depending on the nature of the soil and on the previous climate. For example, the soils in the south and east of the UK will change towards those of warm temperate or Mediterranean areas. The calculated mean maximum potential soil moisture deficit (PSMD) exceeds 200 mm in the east of Essex at present (Jones & Thomasson 1985) and a greater deficit could be expected if temperatures increased and rainfall decreased or remained constant. The amounts of irrigation water necessary to sustain the continuous growth of sensitive crops in these areas would increase, and land use could be forced to change.

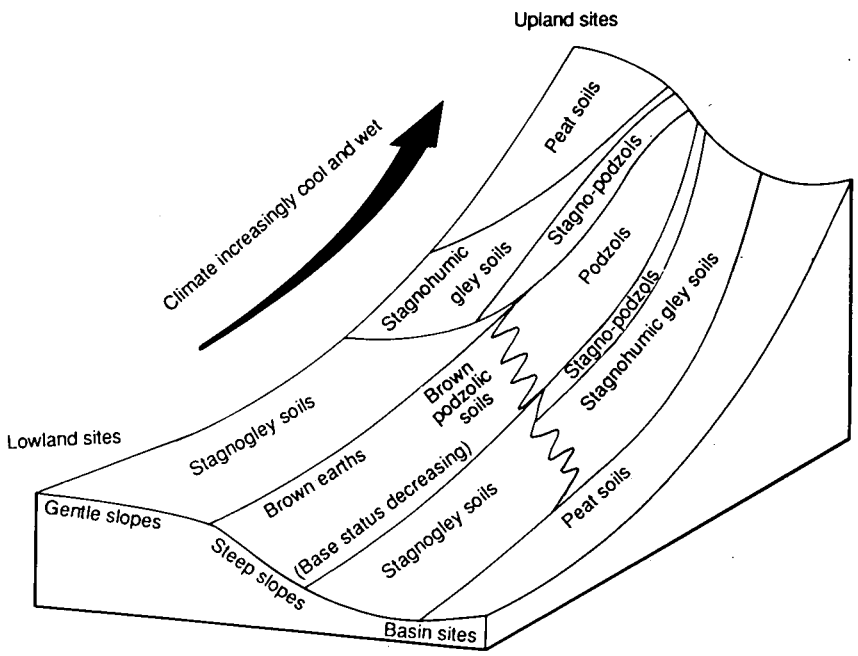

Figure 1. Interactions between climate, relief and soil type in the UK (reproduced by permission of the Soil Survey and Land Research Centre)

In contrast, a heavily waterlogged raw peat soil in the uplands of the UK may normally experience an annual rainfall in excess of 2000 mm, distributed over 200 rain days. The mean annual temperature may well be around 7°C, with a highest mean daily maximum of 22°C and a correspondingly low PSMD, at around 25 mm. An increase in mean annual temperature of 3°C will have very little effect on such a system, where waterlogging dominates soil processes. The hydrology, decomposition processes and mineral weathering will remain substantially unaltered.

In further contrast, an upland stagnopodzol may well be in a poised condition dictated by the hydrological condition of the site, resulting in periods of anaerobiosis. Small increases in temperature, coupled with a decrease in rainfall, may be sufficient to alter aeration of the upper soil horizons, permitting increased soil biological activity and vegetation changes. In turn, the pathways of water movement through the soil would change, leading to increased drying. Eventually, a stagnopodzol may take on the characteristics more associated with a brown podzolic soil.

Longer periods of summer drought may result in irreversible cracking of both lowland clay soils and upland peats. Water pathways will be affected throughout the year and, in the case of peats, greater aeration will permit increased biological activity and nutrient release.

Thus, one cannot assume that all soils will behave in the same fashion as a consequence of climatic change, and it becomes necessary to consider some of the background principles and basic relationships between soil processes and climate in order to make predictions.

3.3 Decomposition processes

It is probable that the most important impacts of climatic change on soils will be on organic matter dynamics. The importance of temperature and soil moisture status in controlling decomposition processes is clearly demonstrated in Figure 2, which

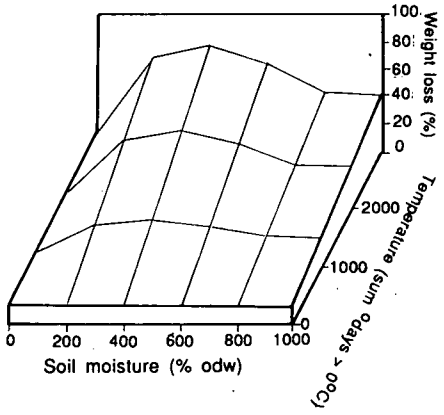

Figure 2. Regression surface showing the interactions between annual weight loss of plant litters, soil moisture status and site temperature

shows that there are strong interactions. For example, weight loss increases that are associated with higher summed temperatures are far more pronounced at 400% soil moisture than those observed at 800% or 1000%.

The balance between organic matter productivity and decomposition will determine whether soils accumulate or lose organic matter as a consequence of climatic change. Both productivity and decomposition will be affected by climatic change, and it is the differential response of these two processes which will dictate the overall changes in soil organic matter. Although there are many interactions which add to the overall picture – such as the effect of enhanced CO_2 on plant productivity and changes in litter quality – the basic picture can best be appreciated by considering the responses of both productivity and decomposition to changes in temperature and rainfall.

Actual evapotranspiration (AET) is an extremely useful climatic index for biological systems because it provides a measure of the simultaneous availability of water and energy in an environment. AET has been found both by research scientists modelling primary productivity (Rosenzweig 1968; Lieth 1975) and by those involved in decomposition studies (Meentemeyer 1978; Berg, Jansson & Meentemeyer 1984; Ineson, Bacon & Lindley 1988) to be an environmental variable clearly linked to biological activity. Figure 3 shows the interaction between above-ground primary productivity and actual evaporation, as demonstrated by Lieth (1975), across a large number of ecosystems. It is clearly not a linear relationship and is best described by the equation:

$$P=3000(1-e^{-0.0009695(AET-20)})$$

where P is annual primary productivity ($g\,m^{-2}$) and AET is the actual evapotranspiration (mm), as calculated by Thornthwaite and Mather (1957). A similar, non-linear, relationship has been found by Rosenzweig (1968) for a wide range of climax ecosystems.

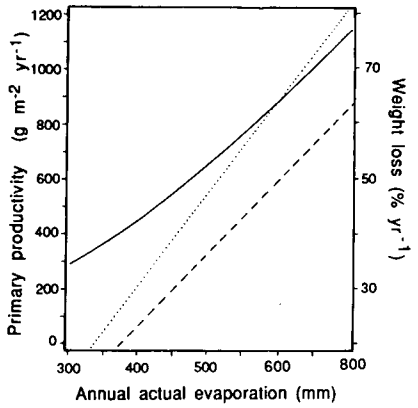

Figure 3. Relationship between actual evapotranspiration and
i. primary productivity (——) (Lieth 1975);
ii. weight loss of deciduous forest litter (·····) (Meentemeyer 1971);
iii. weight loss of coniferous litter (- - - -) (Berg *et al.* 1983)

Others have reported a linear relationship between decomposition rate and AET, although the slope of the line differs for different litter types. Figure 2 shows examples of the relationship between percentage weight loss per year against AET for Scots pine (*Pinus sylvestris*) needles (Berg *et al.* 1984) and deciduous litter (Meentemeyer 1971).

The important point to note is that increases in AET should be associated with both increases in productivity and increases in the rates of decomposition of leaf litter. However, the two relationships do not run parallel to one another and suggest that, for a given rise in AET, increases in decomposition will normally exceed corresponding increases in productivity.

For example, consider Meathop Wood in Cumbria, which is one of the most highly studied woodlands in the UK. The current AET has an average value of 600 mm, and productivity has been measured as $1013\,g\,m^{-2}\,yr^{-1}$ (Satchell 1971), which is in very close agreement with the estimate of $1123\,g\,m^{-2}\,yr^{-1}$ calculated from the relationship of Lieth, given in Figure 2. The system is considered to be at steady state, with no net change in soil organic carbon (Harkness, Harrison & Bacon 1986), or in canopy carbon content. Calculations of AET, using Thornthwaite and Mather (1957), and assuming a 3°C rise in temperature and a 10% increase in rainfall by the year 2050, suggest an increase in AET of around 50 mm by that year. Based on the relationships shown in Figure 2, the estimated productivity should, therefore, increase from 1123 to $1197\,g\,m^{-2}\,yr^{-1}$, whilst the decomposition rate (using the Meentemeyer broadleaf relationship) could be expected to increase from 64% to 72% weight loss per year. The net annual gain of the soil in organic matter from litter would, therefore, decline from an estimated 408 to $335\,g\,m^{-2}\,yr^{-1}$, resulting in a reduction in organic matter content of the soil. Added to this loss are any increases in soil respiration resulting from climatic effects on the existing soil organic matter.

Such calculations assume that the links between AET and productivity/decomposition are causative, and ignore, for example, the effects of possible interactions of increased atmospheric CO_2 on productivity. However, although these calculations are simplistic, they do suggest that moderate changes in the climate may result in important changes in the balances between production and decomposition in ecosystems. Such changes will inevitably affect the organic matter status of the soil. Additional calculations based on these principles suggest that the balance between decomposition and production will not alter consistently across all AET ranges; a 'break-point' exists at around 500 mm AET, below which an increase in AET favours organic matter accumulation, and above which an increase in AET will

result in the loss of soil organic matter.

In many upland systems in the UK, primary productivity is limited by the ability of the soil to mineralise nutrients held in soil organic matter. Increases in the decomposition rate of soil organic matter will give rise to increased growth, and will confound the preceding simplistic analysis. However, the net result of climatic change in such areas is likely to be improved plant growth and nutrition.

3.4 Mineral weathering

The rate of chemical weathering of rocks and minerals is influenced by the nature of these materials, the chemistry of weathering fluids, climate and organic activity (Colman & Dethier 1986). Increased temperatures will certainly result in faster chemical weathering rates and the consequent release of nutrients from primary minerals. In addition, increased soil CO_2 concentrations will slightly depress soil solution pH when dissolved in water:

$$CO_2 + H_2O = HCO_3 + H^+$$

The protons generated will contribute to mineral weathering, as will the protons produced by the dissociation of organic acids formed during organic matter decomposition. However, the additional release of nutrients from minerals by these various weathering processes will be small, compared with the effect of changes in organic matter dynamics.

3.5 Direct effects of elevated CO_2

The direct effects of increased atmospheric concentrations of CO_2 on soil processes are likely to be small. The CO_2 concentrations occurring in soil are usually much greater than atmospheric concentrations, due to the production of CO_2 by the organisms involved in decomposition (Boynton & Compton 1941). Many soil organisms are unaffected by even very high concentrations of CO_2, and certain soil animals and fungi have either adapted to withstand very high levels of CO_2, or are even stimulated by them (see Swift, Heal & Anderson 1979). Similarly, the small increases in CO_2 concentrations in the atmosphere are well below those affecting soil acidity and the leaching of cations.

However, increased soil CO_2 concentrations which may result from increased rates of organic matter decomposition may potentially cause a slight depression in soil solution pH and an increase in alkalinity (Reuss & Johnson 1985). The increased alkalinity would be in the form of bicarbonate, but its concentration, and leaching ability, would be small compared with that of strong acid anions in most soils.

3.6 The role of soils in trace gas release

Soils are important sources of several gases associated with climatic change, namely CO_2, CH_4 and NO_x. Soil micro-organisms and fauna release CO_2 as a major product of decomposition in aerobic conditions, and there is a surprising consistency in the rates of soil CO_2 release reported by a variety of workers in a range of ecosystems. A typical rate of release is around 700 g C m^{-2} yr^{-1}, although this figure can be increased markedly by disturbance or a change in land use (Bouwman 1989).

Soils are a major global pool of carbon, with an estimated 2000×10^{15} g C stored in soil (Bouwman 1989). (See also Chapter 1.) This value compares with an annual increase in the atmospheric pool of 3.5×10^{15} g C, representing an annual atmospheric concentration increase equivalent to 0.5% (Bouwman 1989). A decrease in the soil pool of 0.1% would be approximately equal to a 1 ppm change in the atmospheric concentration of CO_2.

The release of CO_2 from soils is affected markedly by changes in temperature and moisture, as reflected in the decomposition/AET relationships outlined above. In general, changes in soil temperature and moisture content interact in non-linear ways, and the weight losses presented in Figure 2 occur largely as a consequence of CO_2 release.

The quantitative importance of soils in the production of CH_4 and NO_x are discussed in Chapter 2, and it is apparent that soils are of major importance in the generation of these two gases. Of particular concern with regard to climatic change are the potential feedbacks, in which increases in soil temperatures and alterations in the soil moisture content will affect production rates of these gases from soils. Thus, a reduction in the soil carbon pool because of changes in climate may accelerate the increase in atmospheric carbon dioxide, which will, in turn, lead to warming and further changes in the soil pool. Similar concerns are also being voiced with regard to the production of CH_4 and N_2O by soils, because the production rates of these gases are also dependent on soil temperature and moisture status.

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4. Carbon dioxide and plant physiological processes

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4.1 Introduction

This Chapter discusses the influence on plant processes of an increase in atmospheric CO_2 concentrations from the current value of approximately 350 $\mu l\,l^{-1}$ to 500–700 $\mu l\,l^{-1}$, as is expected to occur by the end of the 21st century. The literature documenting past increases in atmospheric CO_2 concentrations (Neftel *et al.* 1985) and modelling future increases (Keepin, Mintzer & Kristoferson 1986) will not be reviewed.

Figure 1 highlights the central role for CO_2 in the growth and physiology of plants. Here, emphasis will be given to the major processes affected by CO_2 concentration, highlighting the future research requirements. Only terrestrial higher plants will be considered, and only those having the C_3 mode of CO_2 fixation.

4.2 Photosynthesis

In the majority of short-term experiments (less than three months), an increase in CO_2 concentration has resulted in increased assimilation rates of between 10% and 150% (Table 1). The cause of this increase is three-fold. First, CO_2 acts as an activator of the primary carboxylation enzyme ribulose bisphosphate carboxylase-oxygenase (rubisco), in a slow, reversible reaction. Second, CO_2 is a substrate for this enzyme. Third, enhanced CO_2 decreases photorespiratory losses of fixed CO_2.

There are some notable exceptions to this enhancement response (Table 2), and several reasons for a decrease in photosynthesis in response to elevated CO_2 levels have been proposed. These include starch accumulation in the leaves, decreased quantum efficiency, decreased amounts and/or activity of rubisco, sequestration of phosphate as sugar phosphate, and the lack of a sustained active sink for assimilate. This latter point is particularly pertinent to experiments conducted with perennial plants growing for extended periods (greater than one growing season) in small volumes of soil. In a recent review, Cure and Acock (1986) showed that the weighted average short-term CO_2 exchange rate response was +52%, whereas for long-term studies the stimulation was +29%. In soya bean, cotton, wheat, rice and barley, a generalised picture emerged of a steady decline in the magnitude of the stimulation of CO_2 exchange rate in response to elevated CO_2 levels (Cure & Acock 1986) – a result attributed to a decline in sink strength (Peet, Huber & Patterson 1985) or reduced nutrient availability.

Assimilation responses to CO_2 levels are extremely sensitive to environmental factors, including light, temperature and vapour pressure deficit (VPD) (see below).

4.3 Stomatal conductance

The average response of stomatal conductance (g_s) to a doubling of the CO_2 level is a decrease of 10–60%, although significant exceptions occur (see below). Possible causes of this decrease in g_s are that CO_2 acts directly upon the guard cell plasmalemma ion pump, and/or that

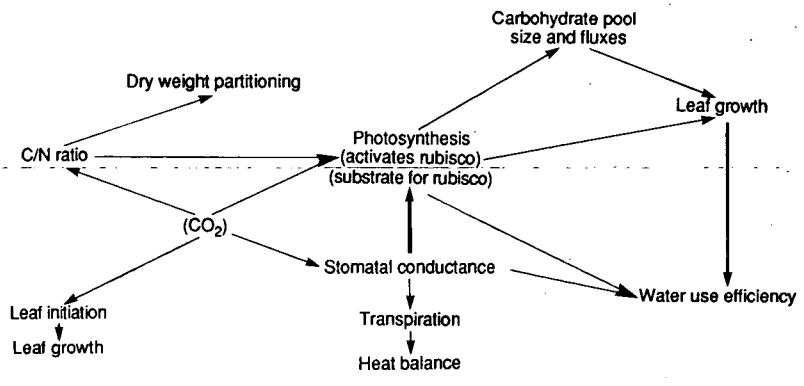

Figure 1. The role of CO_2 in the growth and physiology of plants.

Table 1. Some of the recent work showing an enhanced assimilation rate in response to elevated CO_2

Species	% change in assimilation due to elevated CO_2	Elevated CO_2 used (ppmv)	Author
Sweet gum (*Liquidambar styraciflua*)			
– high light	17–66	675, 1000	Tolley & Strain 1984
– low light	20–100		
Red beech (*Nothofagus fusca*)	45	620	Hollinger 1987
Norway spruce (*Picea abies*)	67	1650	Mortensen & Sandvik 1987
Shagbark hickory (*Carya ovata*)	*c* 80	700	Williams *et al.* 1986
Tulip-tree (*Liriodendron tulipifera*)	*c* 80		
Silver maple (*Acer saccharinum*)	*c* 80		
Green ash (*Fraxinus lanceolata*)	*c* 30		
Red oak (*Quercus rubra*)	*c* 80		
Loblolly pine (*Pinus taeda*)			
– high light	0–50	675, 1000	Tolley & Strain 1985
– low light	10–20		
Douglas fir (*Pseudotsuga menziesii*)	32	620	Hollinger 1987
Oleander (*Nerium oleander*)	50	660	Downton, Grant & Loveys 1987
Rye-grass (*Lolium perenne*)	46	631	Nijs, Impens & Behaeghe 1989
Rat-tail plantain (*Plantago major*)	*c* 20	700	Poorter & Lambers 1988

Table 2. Some of the recent work showing an inhibition of assimilation rate in response to elevated CO_2

Species	% change in assimilation due to elevated CO_2	Elevated CO_2 used (ppmv)	Author
Runner-bean (*Phaseolus vulgaris*)			
– saturating light	*c* −25	1000	Ehret & Jollife 1985
– low light	0.0		
Cotton (*Gossypium hirsutum*)	−15	675	Delucia, Sasek & Strain 1985
Dwarf birch (*Betula nana*) (high nutrient)	−21	675	Oberbauer *et al.* 1986
Labrador tea (*Ledum palustre*) (low nutrient)	−13	675	
Black poplar (*Populus euroamericana*)	−29	660	Gaudillère & Mousseau 1989
Balsa (*Ochroma lagopus*)	−49	675	Oberbauer, Strain & Fetcher 1985
Beach pine (*Pinus contorta*) (CO_2-saturated)	− 5	1000	Higginbotham *et al.* 1985
Sweet gum (*Liquidambar styraciflua*)			
1–4 weeks	41	675	Tolley & Strain 1984
4–8 weeks	33		
8–12 weeks	22		
12–16 weeks	−15		

CO_2 concentration influences guard cell apoplast pH. The net effect of a decrease in conductance, with or without increased assimilation, is an increase in water use efficiency (WUE), defined as the amount of water transpired per unit CO_2 fixed. An increase in WUE per unit leaf area can have significant benefits to plants in the field where water is frequently limiting. However, it should be noted that the total water transpired per plant and per unit area of crop can increase, despite an increase in WUE per unit leaf area, because elevated CO_2 frequently results in a greater total leaf area per plant.

Not all studies report decreased g_s in response to elevated CO_2 levels. Tree species, in particular, show considerable variation in stomatal responses, which are also greatly influenced by the environment (see below).

In addition to changes in conductance caused by variation in stomatal aperture, elevated CO_2 levels can influence stomatal density. Woodward (1987), Woodward and Bazzaz (1988) and Oberbauer, Strain and Fetcher (1985) have shown decreased stomatal density in response to growth at elevated CO_2 concentrations for a range of tree and herbaceous species. Interestingly, Woodward and Bazzaz showed that trees originating from higher altitudes exhibited a greater decline in stomatal density in response to elevated CO_2 than trees originating from a lower altitude.

4.4 Environmental interactions with elevated CO_2

Elevated CO_2 levels ameliorate the effect of drought stress, so that the percentage increase in dry weight following a period of drought is greater than at ambient CO_2 levels. This effect is attributable to greater root mass and enhanced water use efficiency. A possible influence of elevated CO_2 on osmoregulatory processes remains untested, although a more negative solute potential in trees grown in elevated CO_2 levels has been noted (Tolley & Strain 1985). Electron flow

subsequent to Photosystem II was affected adversely by drought, at ambient CO_2, but not in plants maintained at 660 $\mu l\, l^{-1}$ CO_2 (Conroy *et al.* 1986). However, not all species show this stress-ameliorating effect of elevated CO_2 levels.

Mineral nutrition influences the response of many species to elevated CO_2. With adequate phosphorus, the photosynthetic rate of Monterey pine (*Pinus radiata*) was increased by 221% in response to doubling the CO_2 concentration, but, with insufficient P, photosynthesis decreased by 21%. Acclimation of the trees to low P supply occurred after 21 weeks in ambient CO_2, but did not occur in conditions of elevated CO_2. Structural changes in the chloroplast thylakoid membranes, with concomitant decreased ability of the photon-harvesting proteins to trap and transfer energy, were pinpointed as the basis of the P effect (Conroy *et al.* 1986).

In many studies of crop species, the complete nutrient status of the plants was diluted (whereby the increase in total plant volume exceeds the increase in total ion content, so that the ions are diluted in the plant). This dilution significantly reduced the overall stimulation of assimilation induced by elevated CO_2 (Cure & Acock 1986).

Light and temperature are additional environmental factors that modulate plant responses to elevated CO_2 levels. Cure and Acock (1986) noted that high light levels increased the response to CO_2 (relative to lower light flux densities) in about one third of the studies, decreased it in about one third, and had no effect on the final third. The *absolute* enhancement of assimilation is greatest under light-saturating conditions, but the relative enhancement varies, as noted above. An increase in relative enhancement at sub-saturating light levels is caused by a decrease in the light compensation point with an increase in CO_2 concentration, resulting from increased apparent quantum efficiency. These light-modulated responses may be particularly significant in woodlands and closed crop canopies, where a significant proportion of the total leaf population is at low light levels.

The enhancement of assimilation in response to elevated CO_2 increases with increasing temperature. The temperature optimum for assimilation is higher in plants grown at elevated CO_2. The thermal stability of phosphoenol pyruvate carboxylase-oxygenase increases in response to elevated CO_2 in C_4 weeds, and the thermal tolerance of western yellow pine (*Pinus ponderosa*) increased after growth at elevated CO_2, although this increase may be an experimental artefact.

Stomatal conductance responds to a large array of endogenous and exogenous factors, including temperature, vapour pressure deficit, light flux density, abscisic acid, CO_2 level, indolyl acetic acid and root/shoot water status. Growth history also influences stomatal responses to many of these variables (Eamus 1986). In Monterey pine grown at elevated CO_2 levels, stomatal sensitivity to CO_2 increased (Hollinger 1987). As light intensity increases, stomatal sensitivity to CO_2 may increase or decrease, whilst abscisic acid, the hormone responsible for stomatal closure in response to drought, appears both to require the presence of CO_2 to manifest its effect (Eamus & Narayan 1989) and to increase stomatal sensitivity to CO_2. Growth at elevated CO_2 also influences stomatal responses to Δw (the difference in water vapour pressure between leaf and atmosphere) in some tree species (Hollinger 1987), such that the relative closure induced by a stepwise increase in Δw was less at elevated CO_2. Temperature also modifies the response of stomatal conductance to Δw (Johnson & Ferrell 1983).

It is clear from this brief précis that long-term predictions of assimilation and conductance (and hence water use efficiency) responses to elevated CO_2 are fraught with difficulties, principally because the interactions between elevated CO_2 and the major environmental field variables (temperature, VPD, nutrition, light intensity and water availability) remain poorly understood.

4.5 Respiration

Gifford, Lambers and Morison (1985) showed that high CO_2 levels decreased the rate of respiration of wheat. This result was observed for both whole plant and excised root systems, and there was evidence that the alternative cyanide-resistant pathway of respiration was less engaged in plants grown in elevated CO_2. Mung bean roots, in contrast, showed no effect of elevated CO_2 upon respiration, whereas sunflower root respiration was increased. Little is known about the influence of elevated CO_2 upon the various partial processes of respiration or on the partitioning of carbon amongst them (Tolbert & Zelitch 1983). There is evidence that, when sucrose accumulates in leaves, the leaf CO_2 compensation point increases, reflecting an increase in respiratory CO_2 production (Tolbert & Zelitch 1983).

4.6 Growth

Growth responses to elevated CO_2 have generally been positive, but extremely variable. Broadleaved trees and conifers increase in growth by 20% to 120% (Eamus & Jarvis 1989), although Douglas fir (*Pseudotsuga menziesii*) was a notable exception. However, in the majority of these tree studies, the relative growth rates were low, indicating far from ideal conditions during the experiment. In these studies, leaf number, leaf area, leaf weight and leaf weight per unit area were increased in response to elevated CO_2 (Eamus & Jarvis 1989). The suggestion that leaf initiation *per se* is sensitive to CO_2 concentration remains untested. An increase in root weight has also been observed, especially when nutrients are added experimentally. In these cases, the root/shoot ratio generally decreased or remained constant. However, when nutrients were limiting, a substantial increase in the root/shoot ratio occurred, a result ascribed to a plant response to an increased C/N ratio within it (Eamus & Jarvis 1989).

A general conclusion from these measurements of growth is that elevated CO_2 primarily leads to

plants getting larger more quickly, and that the majority of the changes observed are normal ontogenetic changes. In a recent review of crop plants, biomass accumulation among C_3 grasses averaged approximately +28%, and broadleaved crops appeared to be slightly more sensitive to elevated CO_2 than grasses (Cure & Acock 1985).

Squire and Unsworth (1989) concluded that, on average, a doubling of the present CO_2 levels in controlled environment chambers has resulted in a 30% increase in dry matter and yield of a range of crop plants. Using modelling and model parameters derived from controlled environment experiments, they concluded that, in the absence of any change in temperature, a doubling of CO_2 concentrations would increase UK yield by approximately 25% for winter wheat and potato. However, if temperature increased by 3°C, this growth enhancement would be negated for wheat, but the yield of potato would be enhanced by 50–75% of its present value. These models served to highlight both the need for care in extrapolation between species, and the importance of the interaction between various climatological factors.

Elevated CO_2 levels can compensate substantially for the impact of environmental stress. Compensation for low levels of light and nutrients and for water stress in seedlings may enhance their ability to grow and become established. Clearly, if this effect varies between species, species competition and hence natural or unmanaged ecosystem structure and composition may be expected to change. Williams *et al.* (1986) grew three upland and three lowland species together, and both quantum flux density and CO_2 level directly influenced the *relative weight* of each species in a complex way. Tolley and Strain (1984) predicted changes in old field secondary succession from observations of sweet gum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*) grown at elevated CO_2.

4.7 Microbial activity

Mineral nutrient availability is affected by the activity of bacteria and fungi. Norby (1987) investigated the influence of elevated CO_2 on the nodulation and nitrogenase activity of three nitrogen-fixing woody species growing in a fertile forest soil. He found that the total nitrogenase activity per plant increased because of a larger root system. However, specific activity per unit weight of nodule was not influenced by elevated CO_2. Symbiotic nitrogen fixation is closely linked to photosynthetic capacity, and Norby concluded that the observed increase in nitrogenase activity per unit leaf area resulted from the increase in photosynthesis observed in response to elevated CO_2. O'Neill, Luxmore and Norby (1987) also observed increased mycorrhizal symbiosis caused by elevated CO_2, possibly resulting from increased root exudation of carbohydrate under conditions of elevated CO_2 (Norby *et al.* 1987). Because the contribution of nitrogen fixation to the total nitrogen budget of trees increases with age, a small increase in nodulation in young trees may have had significant long-term effects. The frequent observation of increased carbon allocation to roots and the concomitant increased root exudation during growth at elevated CO_2 may be expected to stimulate rhizosphere microbial and symbiotic activity, and hence nutrient availability, although conclusive proof of this stimulation has yet to be provided.

4.8 Future directions

From the available data, three specific research priorities can be pinpointed.

i. Long-term (greater than one growing season) studies are needed of the response of plants to elevated CO_2 concentrations. The interaction of climate (especially temperature and nutrient availability) with elevated CO_2 needs to be investigated using experimental protocols that do not repeat the problems associated with previous short-term studies. Mechanisms of action of elevated CO_2 and the impact of adaptive processes in modulating growth responses require study.

ii. The temperature and growth response functions of UK agricultural species need to be elucidated. The interaction of climatic factors (VPD, rainfall, etc) with elevated CO_2 in the control of growth and yield requires study in environments that are as close as possible to future climate scenarios. Realistic temporal variation in these climatic factors needs to be incorporated into growth studies.

iii. Future crop species (including trees) and cultivars need to be identified. Significant changes in climate (including CO_2 levels) may be expected to result in a change in the species/cultivars that grow optimally in the UK.

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5. Forests

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5.1 Introduction

Any climatic change that occurs over the next 50 years will occur within the lifetime of many of the trees now growing in the UK. There will be insufficient time to change the species or provenances to keep pace with the changing climate. Consequently, trees may be more affected by 'greenhouse' warming than other plant species. Trees are especially vulnerable to any change in the frequency or severity of extreme events, such as gales, droughts or frosts, because these events destroy biomass that has built up over many years.

An increase in temperature is likely to have a greater effect on forests than on many arable crops for two other reasons. First, much of the UK forest estate occurs in the uplands, where growth is regulated strongly by temperature, and where the rate of release of nutrients from organic soils is greatly affected by temperature. Second, forests are aerodynamically rough, so that the temperature of the foliage is very close to the temperature of the air: this is not so for short vegetation where leaf temperatures are more influenced by windspeed and solar irradiance.

5.2 Natural distributions of species

In the UK, a difference of 2°C in mean summer temperature represents about 400 km of latitude or 300 m in altitude. Thus, any change in mean temperatures of even 0.5–1.0°C is likely to shift the potential boundaries of tree species quite substantially.

The fossil pollen record shows an effect on the distribution of tree species during the warmest part of the present interglacial, 4000–8000 years ago. At that time, Europe may have been about 1°C warmer than at present. Deciduous forest was predominant in England, consisting of alder (*Alnus* spp.), elm (*Ulmus* spp.), hazel (*Coryllus avellana*) and lime (*Tilia* spp.), with birch (*Betula* spp.) occurring more in the north and west. Pine (*Pinus* spp.) had become scarce in England and was common only in the northern half of Scotland (Lamb 1977). Scots pine (*Pinus sylvestris*) stumps, dated 4000 years before the present, occur in peat deposits in the Cairngorm Mountains at about 790 m above sea level, well above the present tree-line of 620 m (Pears 1975). At that time, Norway spruce (*Picia abies*) grew in the high Alps in areas now occupied by the more hardy Arolla pine (*Pinus cembra*) (Zukrigl 1975).

In recent times, also, changes have been observed at the tree-lines. In Canada, white spruce (*Picea glauca*) has expanded northwards in the Hudson Bay area in response to warming in the period 1920–65 (Payette & Filion 1985), while Scots pine populations in the mountains of Sweden may have declined in response to cooling in north-west Europe in the period 1965–80, as well as in response to atmospheric pollution.

The natural distributions of some native tree species in Britain seem to be determined by temperature. The small-leaved lime (*Tilia cordata*) does not regenerate naturally north of the Lake District, apparently because the temperatures are too cool in spring for pollen tube growth (Piggott & Huntley 1978, 1981), while the bird cherry (*Prunus padus*) is found almost exclusively in northern and upland Britain. Cannell, Grace and Booth (1989) list many broadleaved species which might spread northwards following climatic warming, and those species currently growing in more southerly regions of Europe and elsewhere that might grow well in southern England.

Most of the exotic conifers planted in the uplands, like Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*), have large natural ranges. In general, the areas that provide the best seed possess climates that match those in Britain (with some notable exceptions). Following climatic warming, the best seed origins might be places which are warmer than Britain now, although the climate in those places will change too. More worrying is the possibility that the results of tree breeding may be of limited value if the climate changes substantially in the 50–80 year interval between progeny testing and the growth and

harvesting of the genetically improved trees.

5.3 Effects of forest soils

As mentioned above, forest growth in the uplands will be greatly influenced by the effect of climatic warming on soil properties. Models of the growth of north-eastern North American forests suggest that climatic warming will increase the productivity of forests in those areas where soil water is not limiting and nitrogen availability is enhanced, but warming will decrease productivity where water becomes more limiting (Pastor & Post 1988). In Britain, if we assume that soil water is not limiting, a temperature rise in summer from, say, 14°C to 17°C is likely to increase the rate of breakdown of litter and nutrient release by 10–30% (see Chapter 3).

5.4 Direct effects of increased levels of CO_2

Overall, the direct effects of doubling CO_2 concentrations on tree growth are likely to be positive, but less important than the temperature rise that will occur by the time CO_2 levels double, along with the increase in the other greenhouse gases. Eamus (Chapter 4) outlines the effects of elevated CO_2 levels on increasing photosynthesis, decreasing stomatal conductance, and increased growth. However, over a period of years, trees may acclimatise to high CO_2 levels by reducing the number of stomata and reducing the activity of the photosynthetic enzyme, rubisco. Also, responses to high CO_2 levels will depend upon the levels of nutrient and water, and there is at present no way of extrapolating the results of studies on seedlings to forest stands.

5.5 Potential increase in forest growth

The work of Mikola (1962) on the annual rings of Scots pine in Finland over the period 1880–1960 enables a linear regression to be calculated between radial growth and July temperatures. This regression suggests that a 3°C rise in July temperature over the range 14–17°C could increase radial growth by 54% over present-day values. There is a marked increase in general yield class of Sitka spruce with decreasing altitude in Scotland (Worrell 1987). If it is assumed that this increase is due mainly to temperature, and that mean temperatures increase by 0.7°C with every 100 m decrease in altitude, it is possible to speculate how the general yield class of Sitka spruce might change as a result of climatic warming or cooling (Figure 1). An average site now producing $14\,m^3\,ha^{-1}\,yr^{-1}$ at 400 m might produce $20\,m^3\,ha^{-1}\,yr^{-1}$ if temperatures rose by only 1°C.

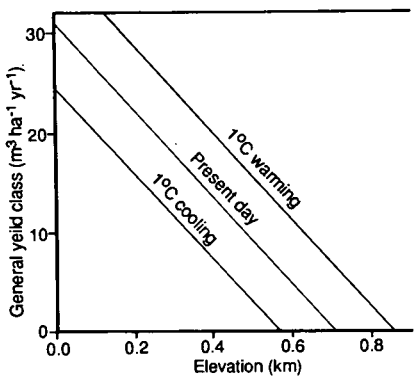

Figure 1. Present-day relationship between the timber yield of Sitka spruce plantations and elevation in northern Britain (from Worrell 1987) and possible future relationships given a 1°C warming or cooling (from Cannell *et al.* 1989)

5.6 Changes in phenology

The buds of most woody perennials (like many seeds, bulbs, etc) need to be chilled in winter to release dormancy. If the buds are not fully chilled, they will require a large thermal time (heat sum, in day degrees) to grow to budburst, and growth will be late, and may be poor or abnormal. Studies on 15 woody species in Britain showed that species like Sitka spruce and beech (*Fagus sylvatica*), which flush relatively late, have a high chilling requirement and are likely to flush equally late after warm winters (Cannell & Smith 1986; Murray, Cannell & Smith 1989). By contrast, species like hawthorn (*Crataegus monogyna*) and some poplars (*Populus* spp.), which flush early at present, are likely to flush even earlier given warm winters and springs (Figure 2). This prediction

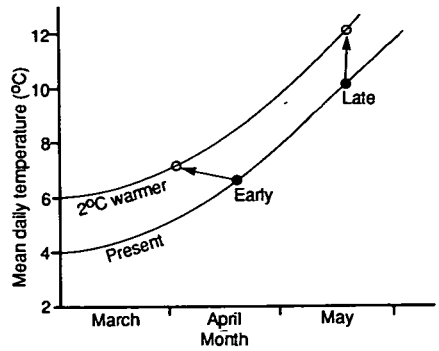

Figure 2. Diagrammatic representation of the effects of a 2°C warming on the dates of flushing (budburst) of tree species that flush early or late at present. Early flushing species may be even earlier, while late flushing species may remain late

was borne out to some extent in the spring of 1989 (J M Sykes pers. comm.). Growth cessation, leaf fall and frost hardening in the autumn are all triggered by shortening daylengths, as well as by cool temperatures. In warmer conditions, many native tree species may cease growth 'too early' in the autumn and fail to take advantage of prolonged mild conditions. In maritime climates, a 1°C rise in mean temperatures prolongs the growing season more than in continental climates.

5.7 Possible adverse effects

Clearly, any increase in peak windspeeds, unseasonal frosts, or increased hazards from pests or fire will be damaging to forests.

If warming exceeds 2°C, it could have adverse effects on forest growth, for reasons that are not understood. The evidence from provenance transfer experiments (movements of tree seeds from different sources) suggests that some populations adapted to cool climates perform poorly in warmer climates (see Cannell *et al.* 1989).

If it becomes drier, there will almost certainly be adverse effects on tree growth, as evidenced following the summers of 1976 and 1989 in England. Photosynthesis of Sitka spruce (a species native to the coastal fog belt of western North America) is much reduced in dry air owing to stomatal closure (Jarvis 1986).

The yields of Cox's apple in Kent are strongly negatively related to temperatures in February–April, so that a 1°C rise in mean maximum temperatures in this pre-blossom period might decrease yields by about 1 t ha^{-1} (below current mean yields of 8–12 t ha^{-1}) (Jackson & Hamer 1980).

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6. Natural vegetation

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6.1 Introduction

The spatial pattern in the vegetation of the British Isles is often strongly correlated with climatic variables. In the event of significant departures from the recent climatic record, profound effects can be expected on the native flora, as well as on agriculture and forestry. These effects will appear as changes in the timing of seed germination and flowering, in response to drought, to extremes of winter and summer temperatures, and to changes in the length and distribution of the growing season. A likely consequence will be the expansion of species with a predominantly Mediterranean distribution, recession of species with a northern distribution, extension of lowland species to higher altitudes, and retreat of upland and montane species, the latter already composing a significant element of the present-day rare, vulnerable and endangered flora.

The first effects of climatic change may be subtle alterations in the relative importance of species within existing plant communities, rather than major changes in plant distribution. The rate of vegetation change will be closely related to the lifespan and dynamics of the component plant populations. The most rapid changes may be expected in ephemerals of disturbed habitats; greater inertia will characterise the response of woody vegetation and perennial herbaceous communities on infertile soils.

Throughout the world, the selective effects of climate are expressed as highly varied patterns of natural vegetation, a reflection of the interplay of temperature, rainfall, daylength and seasonality. In Britain, for example, mountain sorrel (*Oxyria digyna*) (Figure 1i) is confined to areas of the north-west where the annual rainfall exceeds 1600 mm, while, in contrast, the stemless thistle (*Cirsium acaulon*) (Figure 1ii) is restricted to regions of south-east Britain with a minimum mean July temperature of 16°C. At lower temperatures, the thistle fails to release significant quantities of seed

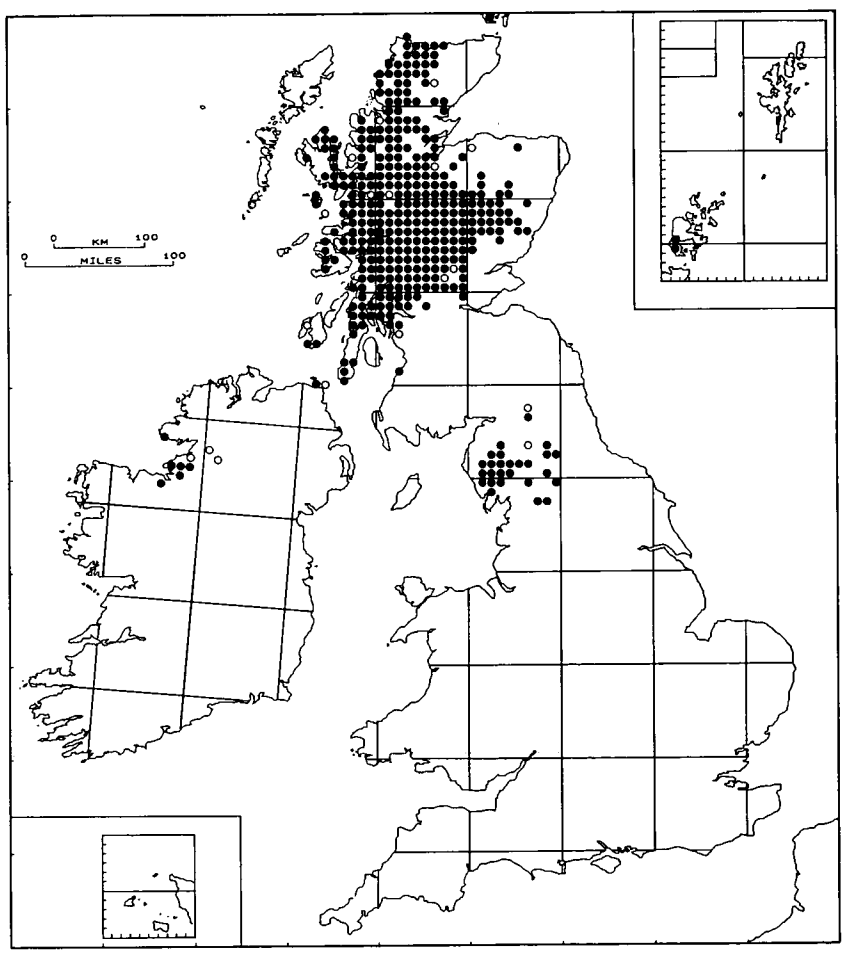

Figure 1i. Distribution of mountain sorrel (*Oxyria digyna*) in the British Isles (from Perring & Walters 1976)

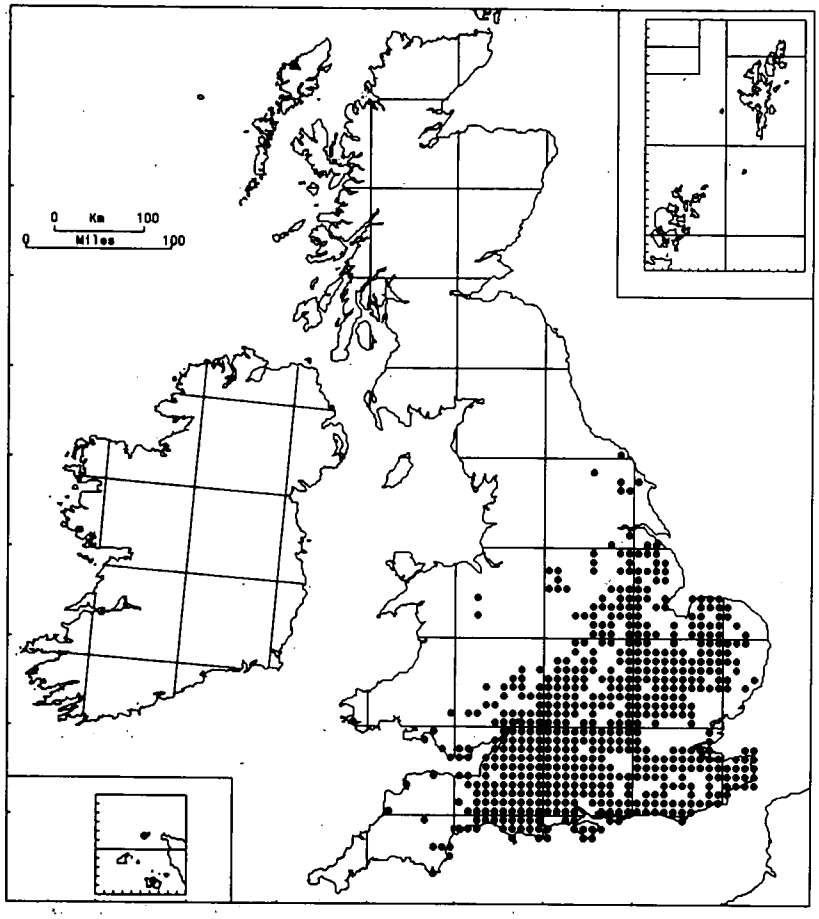

Figure 1ii. Distribution of stemless thistle (*Cirsium acaulon*) in the British Isles (from Perring & Walters 1976)

(Pigott 1974). On a finer scale, pronounced differences in vegetation can be detected between the north-facing and south-facing slopes of neighbouring hills or valley-sides (Perring 1959, 1960), again correlated with differences in soil temperature, persistence of frost, soil moisture and solar irradiance. At Millersdale, north Derbyshire, for example, 2022 germinating seedlings were counted in a standard area of south-facing, dry, open grassland, but in the closed turf of a nearby north-facing slope the numbers were 30% lower over an equivalent area (Table 1) (Hillier 1984). More significantly, 75% of the seedlings on the north-facing slope did not appear until spring, while the majority of seeds on the south-facing side germinated soon after their release in the autumn. Among the non-grasses, the warmer, summer-droughted discontinous turf of the south-facing slope favoured annuals and monocarpic species, while the denser vegetation of the cooler, more continuously moist soils of the north-facing slope favoured perennials. Such localised differences in vegetation functioning are strongly determined by the interaction of climate with topography, and result in a fine mosaic of habitats and vegetation which characterises much of the British landscape.

Table 1. Total number of seedlings recorded on two adjacent slopes of equal area but opposite aspect in autumn and spring over 12 months at Millersdale, Derbyshire (from Hillier 1984)

	Autumn	Spring
North-facing slope		
Grasses	86	160
Annual and biennial forbs	0	12
Perennial forbs	258	873
TOTAL	344	1045
South-facing slope		
Grasses	670	144
Annual and biennial forbs	316	416
Perennial forbs	202	274
TOTAL	1188	834

6.2 Mechanisms of change in vegetation

Precise explanations for many of these patterns are largely unknown and await detailed autecological studies. Some progress has been made, however. For example, the small-leaved lime (*Tilia cordata*) shows a distribution predominantly in the southern half of Britain, yet introduced specimens thrive in the central Highlands of Scotland. In this species, it is not the growth of the sapling or maturing tree which limits distribution, but the temperature sensitivity of seed production (Pigott & Huntley 1981). Below 15°C, pollen germination and tube extension are largely suppressed and embryo maturation is inhibited.

To provide explanations for the often highly specific or limited distributions of a wider range of species and to predict their behaviour in future climates, an experimental programme has been launched at the Unit in Sheffield, in which a large number of ecologically contrasted species are being examined. This Integrated Screening Programme (ISP) combines ecology, physiology, morphology and biochemistry, and involves some 56 specific experimental tests. Several of the tests bear directly on the forecasting of vegetation responses to climatic change (Table 2). Of the 83 species currently scheduled for screening in the ISP, the majority are drawn from the native floras of Britain, north-west Europe and Mediterranean countries.

6.3 Vegetation response to changing temperatures

As an illustration of the data generated by the ISP, Table 3 summarises the growth responses of six contrasting species to a range of temperatures. The temperature optima for dry weight yield of two widespread and economically important pasture grasses – sheep's fescue (*Festuca ovina*) and rye-grass (*Lolium perenne*) – are 18.7°C and 19.8°C respectively. The optima of two species with a predominantly south-east distribution – upright brome (*Bromus erectus*) and tor-grass (*Brachypodium pinnatum*) – are

Table 2. A selection of tests from the Integrated Screening Programme (ISP) which are relevant to understanding the effects of climatic change on vegetation

Seed germination at constant temperatures in light and dark
Seed germination at fluctuating temperatures in light and dark
Growth under constant temperature
Growth under fluctuating temperature and drought
Growth under episodes of low temperatures
Growth in elevated CO_2
UV-B radiation tolerance
Water consumption
Root penetration
Reserve carbohydrates
Structural responses to changes in daylength and chill
DNA (genome size)
Flowering under drought

Table 3. Optimum temperature for maximum yield (dry weight) of 28-day-old plants. Illumination 125 $\mu E\,m^{-2}s^{-1}$ (from Hunt & Neal 1988)

Species	Temperature optimum (°C)
Sheep's fescue (*Festuca ovina*)	18.7
Rye-grass (*Lolium perenne*)	19.8
Upright brome (*Bromus erectus*)	20.2
Tor-grass (*Brachypodium pinnatum*)	20.9
Fat hen (*Chenopodium album*)	24.0
Stinging nettle (*Urtica dioica*)	26.9

20.2°C and 20.9°C, while the annual species of disturbed soils and waste land – fat hen (*Chenopodium album*) – has an optimum of 24.0°C and the stinging nettle (*Urtica dioica*) 26.9°C. Such data suggest that some species have the potential for increased yield under warmer summer temperatures, while others will be less favoured.

A second source of predictive information in the ISP derives from measuring nuclear DNA mass. The amount of DNA present in the nucleus can differ more than 1000-fold between different plant species. In Britain, there is a strong correlation between nuclear DNA amount and the time of year when a plant grows (Grime & Mowforth 1982). High DNA content is associated with a large cell size and, in many species, coincides with the ability to store the water-soluble carbohydrate, fructan (Hendry 1987). Such species tend to grow in late winter or early spring by turgor-dependent cell inflation of preformed cells, rather than by concurrent cell division and expansion. Familiar examples include the majority of native grasses and bulb plants characteristic of early spring growth in British pastures, scrub and woodland. Conversely, plants with small cells and low DNA amounts tend to delay growth until early summer. An example of the extent to which growth (leaf extension rates) during early spring can be predicted from determinations of nuclear DNA content is shown in Figure 2 for 24 common native species. By screening plants for DNA amount and fructan content, it is then possible to begin to predict their responses to increased temperature and to forecast changes in the composition of plant communities.

Apart from temperature changes, an important determinant of plant response to climate is rainfall. Although the meteorological predictions need to be refined, it is already forecast by some models that episodes of drought will become a more regular, seasonal, feature of the British climate. Screening plants for their drought tolerance is an area of active research at the Unit.

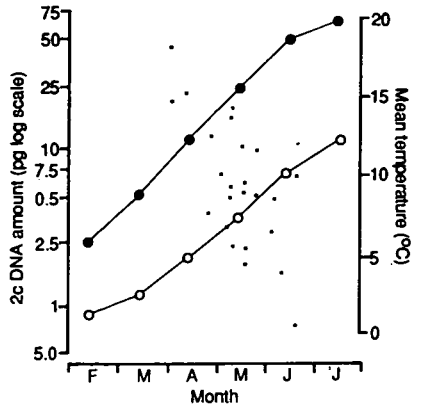

Figure 2. Relationship between nuclear DNA amount (in pg) and month of shoot expansion of 24 plant species, together with the mean daily temperature maxima (●) and minima (○) for Sheffield (1951–80) (from Grime & Mowforth 1982)

6.4 Vegetation response to changing patterns of rainfall

A significant proportion of the British flora, particularly pasture grasses, is not well adapted morphologically, or in life history, to prolonged drought. Instead, many grasses appear to rely on damage limitation and repair through biochemical processes. Many of the slow-growing species of infertile soils synthesise particular antioxidants in response to water deprivation. For example, sheep's fescue and wavy hair-grass (*Deschampsia flexuosa*), two widespread pasture grasses of upland Britain, form large amounts of the tocopherols (vitamin E) on droughting, while annual poa (*Poa annua*) and oat-grass (*Arrhenatherum elatius*) from more productive habitats rely on the antioxidant, glutathione (Price & Hendry 1989). By screening for such biochemical responses to drought, it may be possible to predict the responses of species to extended periods of water shortage.

6.5 Analogues in southern Europe

Attempts have been made in several laboratories to extrapolate from the floras of Mediterranean countries in

order to predict the likely composition of the British flora under warmer temperatures but unchanging rainfall patterns. Such attempts have one fundamental flaw. The daylength in Britain is significantly different from that of southern Europe, particularly at critical periods of winter, early spring and summer (see Figure 3). Aberdeenshire will continue to enjoy nearly three hours more daylight than north Spain in high summer each day, whatever temperature changes occur. In mid-winter, the advantage is reversed. Apart from any change in the length of the growing season at each latitude, it is the conjunction of rapidly changing daylength with temperature which regulates frost hardening, flower initiation, bud development, fruit set, fruit ripening and, ultimately, leaf senescence and abscission. Much of the flora present in Britain today is adapted to an 18 hour daylength at anthesis, and extrapolations from the 14 or 15 hour days of southern Europe may be of limited relevance.

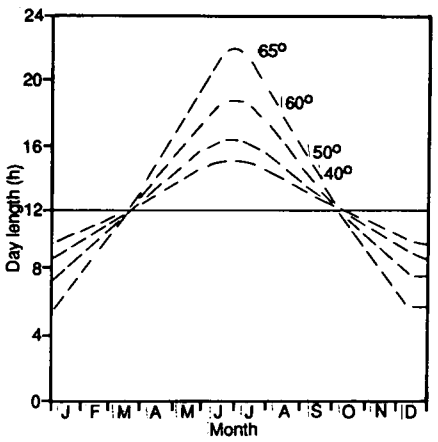

Figure 3. Daylength, including twilight (nautical definition), at various latitudes throughout the year

6.6 Predictions

Bringing together field observation, laboratory-based findings and some insights derived from studies of neighbouring floras, it is possible to obtain broad indications of the expected or probable changes to the natural vegetation of the British Isles (Table 4). Changes in the length and timing of the growing season may be expected, with an overall increase in productivity where moisture and nutrient supply are not severely limiting. An extension of lowland species to higher altitudes with an expansion of 'Mediterranean' species beyond their present limits in southern Britain seems likely. Some rare species will be endangered by such changes, particularly those exclusively confined to north-facing slopes. Others which have a southern limit of distribution in Britain will retreat northwards.

These impacts are relatively long term. The current challenge is to predict the more immediate effects, which are likely to be manifested as subtle changes in the relative importance of plant species within existing communities. At first, these changes will probably occur as temporary departures or unusual episodes affecting plant growth, flowering or senescence in climatically extreme years. For this reason, the monitoring of natural vegetation in the field, against climatic data, has an important role in current efforts to predict how vegetation changes may occur in future climates. Already the prospect of climate change has begun to catalyse some fundamental rethinking of long-established agricultural and forestry practices. A similar change of strategy will be required by those concerned with the management of the natural vegetation and fauna, if the diversity of habitats and the composition of the British wildlife are to be retained over the next decades. The longer-term impact of climatic change on natural and semi-natural vegetation may be expected to interact strongly with the profound changes in the flora which are already taking place as a consequence of land use. The most rapid effects of climatic warming are likely to occur in ephemeral plant populations of fertile, disturbed ground. Slower rates of change may be predicted where the lifespans of the plants are longer and the productivity of the soil is low. Such differential rates of change will result in additions to, or at least territorial expansions of, elements of the British flora. This expansion will occur alongside a further retreat of remnants of the native upland, montane and sub-arctic floras. It is precisely these elements which include a substantial part of the rare plant species of the British Isles. Their future is not assured. Climatic change will prompt a revaluation of conservation priorities and methodology in Britain and beyond.

Table 4. Summarised predictions of the direction of change in vegetation in the British Isles, initiated by climatic change (abridged from Grime & Callaghan 1988)

1. Growing seasons shift to autumn–winter–spring in southern Britain
2. Growing season extended, particularly in northern Britain
3. Overall, higher level of plant production
4. Species currently restricted to south-facing slopes will colonise other aspects
5. Species with a predominantly Mediterranean distribution will show an expansion within Britain
6. Species with a predominantly lowland distribution will expand to higher altitudes
7. Drier habitats will favour species with high nuclear DNA; continuously moist habitats those with a low DNA content
8. Species with isolated populations on damp north-facing habitats will be threatened. Bryophytes and some ferns will be particularly vulnerable
9. Species with a northern distribution limit in the British Isles will advance northwards
10. Species with a southern distribution will retreat northwards

6.7 References

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7. Invertebrates

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7.1 Insect pest abundance

The impact of insects as pests depends upon their abundance, the relationship between insect numbers and damage, and the economics of crop production. It is, therefore, wrong to see the problem of insect pest damage simply as a result of insect distribution. In extreme cases, the mere presence of an insect species is likely to cause economically significant damage, but in most situations crop plant tolerance and the economics of control mean that we are principally concerned with the likelihood of insect numbers passing a critical threshold. We should, therefore, be concerned with the effect of climatic change, mainly temperature rise, on the population dynamics of insect pests.

7.1.1 The effect of temperature on insect physiology and abundance

Many studies have shown that, across a fairly wide temperature range, there is a linear relationship between temperature and insect development, survival, growth and reproduction (Ratte 1984). It may be simply concluded that insect pests will become more abundant as temperatures increase.

It is also possible that higher temperatures will result in the same maximum levels of insect abundance, but that the maximum levels will be reached sooner. Evidence comes from the abundance of rapidly multiplying pest species, such as the aphid pests of annual crops: in warm summers, populations rise and fall faster than in cool summers (Carter *et al.* 1980). This conclusion is, however, probably only of real value in describing insects whose population dynamics are dominated by intraspecific competition, and/or by a tight and simple insect/plant relationship. For example, in a summer with high temperatures, aphid population growth and wheat development are rapid so that the calendar date when competition for a declining food resource reaches a critical level (and emigration becomes pronounced) is reached sooner.

However, the above conclusions rarely hold true. The population dynamics of insect pests cannot be understood by considering the insect alone. To understand and predict the dynamics of insect numbers properly, we have to appreciate the three trophic level nature of insect population dynamics: the abundance of insect herbivores is a function of host plant abundance and quality, and the effects of natural enemies. The next three sections, therefore, consider the insect, its interaction with the host plant, and its interactions with natural enemies.

7.1.2 The effect of temperature on insects: the life cycle perspective

The impact of climatic change can only be appreciated by realising that insect life cycles are rarely simple. Most insects undergo metamorphosis, which results in an adult, an egg, several larval stages, and a pupal stage, each with different susceptibilities to climatic variables. In addition, susceptibility to weather (nutrition, disease, etc) alters during each stage – for example, young larvae are much more susceptible than older larvae.

Neither can we say that a particular stage is tolerant or susceptible to weather in all species. Tolerance depends upon the way the life cycle has evolved in relation to the seasons. For example, different lepidopterous pests spend the winter as eggs, larvae and pupae (Nothangle & Schultz 1987).

Whereas the wintering stage is usually very weather tolerant, the spring stages tend to be vulnerable to variability in weather. Two exceptions are worth noting. First, some species can pass the winter in different stages. For example, aphids usually overwinter as eggs but some species can pass the winter in the egg or the adult/nymphal stage. These active stages tend to be very susceptible to weather. Second, a number of species do not have a spring active stage, being late-season specialists, and they may be more prone to climatic changes that affect the autumnal stages.

To illustrate the way in which climatic warming may affect insect pest numbers mainly through the action of temperature on the pest itself, two examples are presented below.

A rise in winter temperatures would almost certainly lead to a rise in the abundance of aphids like the green spruce aphid (*Elatobium abietinum*) (which overwinters in the adult/nymphal stage in maritime climates) because its survival is strongly affected by temperature (Day & Crute 1990). Where it occurs, it is a severe defoliator (through needle loss), and an upsurge in its numbers on Sitka spruce (*Picea sitchensis*) could be devastating. There are a number of other similar species in other parts of the temperate zone, eg the balsam woolly aphid (*Adelges piceae*) (and the green spruce aphid) in North America.

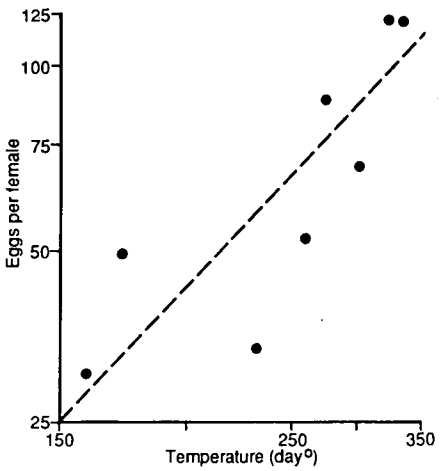

Figure 1. Effect of spring temperatures (March to mid-May) on the fecundity of the pine beauty moth (from Watt & Leather 1988)

A second example relates to spring weather. Emergence of the pine beauty moth (*Panolis flammea*) in Scotland is temperature dependent, and poor weather can delay mating (with a consequent reduction in fertility) and disrupt egg laying. In the field situation, a clear pattern between temperature and realised fecundity can be found (Figure 1) (Leather, Watt & Barbour 1985), and, in outbreak areas, the population dynamics are apparently simple (Watt & Leather 1988), so that it is very likely that climatic warming would lead to an increase in the frequency of outbreaks of this species.

7.1.3 Insect/plant interactions

Two general principles are worth considering: the effect of drought stress on plant 'quality', and the effect of warming on the coincidence between insects and their preferred host stages.

There is a widespread view that drought stress leads to an increase in insect pest attack (White 1984). The logic behind this belief is that drought stress leads to a decline in the plant's defensive chemicals but an increase in nutrient levels, resulting in an increase in insect survival and a consequent increase in population growth (Rhoades 1983). There is some good circumstantial evidence, particularly from long-term records of weather and insect abundance (White 1974). However, detailed studies are few and they tend to point away from the rather simplistic stress/nutrition hypothesis (Watt 1988, 1989a, 1989b). Nevertheless, we might expect that a warmer and drier climate would lead to an increase in the severity of aphid and bark beetle pest outbreaks (Berryman & Stark 1985). Mature foliage-feeding moths and sawflies may also benefit (White 1974; but see Hanski & Otronen 1985; Larsson 1990), but insects adapted to flushing foliage are unlikely to be affected.

Flush-feeding insects are, however, likely to be influenced by climatic warming through phenological synchrony. The winter moth (*Operophtera brumata*), for example, requires a newly burst bud for its survival, and egg hatch and budburst tend to coincide to different degrees in different years (Feeny 1976). The two phenological processes appear to respond differently to temperature (Thomson 1990), and the insect has probably evolved to take advantage of average conditions. Thus, we may conclude that gradual warming will not affect the degree of coincidence between insect pests and their host plants because the selection pressure on the insect is so intense that it is bound to track plant phenology. However, a decrease in climatic variability would certainly lead to an increase in the abundance of flush-feeding insects (and *vice versa*).

7.1.4 Herbivore/natural enemy interactions

Natural enemies play an important role in determining the abundance of insect pests. Weather can affect this role, sometimes in subtle ways. It is generally accepted that high temperatures lead to fast insect development and a decrease in the time available for predators to attack prey species (Price *et al.* 1980). On the other hand, searching parasites often require high temperatures, leaving their hosts relatively unparasitised in cool years. Insect/parasite synchrony can also be as critical as insect/plant synchrony. Moreover, insect disease incidence is affected by temperature, humidity and sunshine.

There is insufficient space in this Chapter to explore fully the effects of climatic change on the many forms of insect/natural enemy interactions. One example may, however, demonstrate how complex the population dynamics of insects can be. Although it was stated above that aphids tend to benefit from mild winter weather, and that poor spring weather is detrimental to most insects, there is evidence to show that high numbers of cereal aphids on summer crops tend to follow particularly cold Aprils (Vickerman 1977). One explanation stems from the fact that the cereal aphids found in the crop in spring come from two sources: eggs or overwintering nymphs and adults. In a mild winter, the active stages overwinter well, build up fast, and attract parasites and predators which by June finally overwhelm the aphid population. After a severe April, only the egg stages survive and these develop into insects which enter the crop relatively free from natural enemies. Whether this explanation is correct has not yet been established, but it illustrates the fact that it can be misleading to consider the effects of climatic change on single organisms without taking into account their interactions with the trophic levels above and below them.

7.1.5 Conclusions

How will climatic change affect insect population dynamics? There are no simple answers. Climatic change will act through its effect on the reproductive rate of pest insects, but, because of its potential effects on host plants and natural enemies, the final outcome is difficult to predict. The best approach is to model the effects of climatic change on pest/host plant and pest/natural enemy interactions, which means a change in direction in insect population ecology. Traditionally, insect ecologists have been those who looked for patterns between weather and abundance, and those who looked for intrinsic regulatory processes. These divergent approaches will not provide a sound basis on which to forecast the effects of climatic change. Both approaches must be combined in a three trophic level approach to insect pest population dynamics, and this combination will only yield fruitful results through population modelling.

7.2 Past and present insect distribution

Studies of the distribution of invertebrates at present and in the past show that climate is a major factor controlling their natural ranges. Fossil deposits of skeletal wingcases show that, during glacial periods, up to 30% of the insect species in Britain were similar to those now found in the tundra (Coope 1970), and the species present during warm interglacials are now typically found in central and southern Europe. This history of changing distribution accounts for the fact that some wingless beetles occur now as relicts in the Spey valley in Scotland, while the winged forms are found only in southern England: similarly, there are beetles on the south coast of England found mainly in southern Europe (Crowson 1981).

The geographical distributions of many species coincide with the distributions of climatic variables. Studies of insect ranges and their controls have been made at the level of whole faunas, such as ants, where July mean temperature, sunshine hours, length of growing season, and boreal or oceanic climate have been shown to be correlated with different zoogeographical regions in northern Europe (Urbani & Collingwood 1977). At the specific level, the psychid moth (*Luffia ferchaultella*), which feeds on lichens and algae on tree trunks, has a range in Britain almost limited by the 16.4°C isotherm for July, the month when the adults emerge and oviposit. Where the range overlaps the 16.4°C isotherm in eastern Britain, there are high sunshine hours. The northern limit is slightly south of the 16.4°C isotherm because cold winters kill the larvae (McDonogh 1939).

Following climatic warming, many of the 20 000 species of insects in the UK would expand their natural ranges, especially as the majority of invertebrate groups occur in the south of Britain where the climate is mildest. Thus, grasshoppers and crickets (Orthoptera) have 31 species within 100 km^2 in southern England, but only four species reach northern Scotland (Figure 2). The preponderance of dragonfly species (Odonata) in southern England can be related to high temperatures in April (Figure 3).

Of the 58 butterfly species that occur in Britain, only eight are present throughout mainland Britain (excluding Ireland, Orkneys and Shetlands), while 45 have a northern range boundary limit and five have a southern limit. In natural conditions, the northern boundaries of many species of birds and mammals are thought to be limited by summer and winter temperatures (Hutchins 1947). The southern boundaries may often be related to a complex of factors, including competition from other species (Macarthur 1972). This principle is likely to apply to invertebrate species, although they may be more dependent on the restricted habitats which they occupy.

The distributions of many insects are limited by the distributions of the plants on which they feed. For example, the rush moth (*Coleophora alticolella*) feeds on the seed capsules of heath rush (*Juncus squarrosus*). At high altitudes, populations of the moth are limited because seed capsule development is poor, and the moth may become extinct in years when seed set fails (Randall 1982). At lower altitudes, the rush moth appears to be held at low

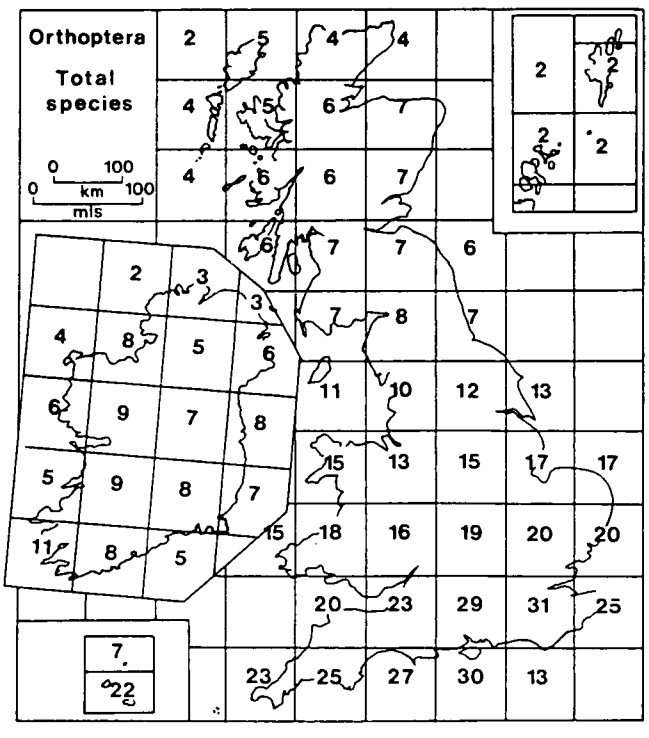

Figure 2. Numbers of species of Orthoptera (grasshoppers and crickets) in the British Isles, showing a concentration of species in the warmer southern areas (data from the Biological Records Centre, ITE)

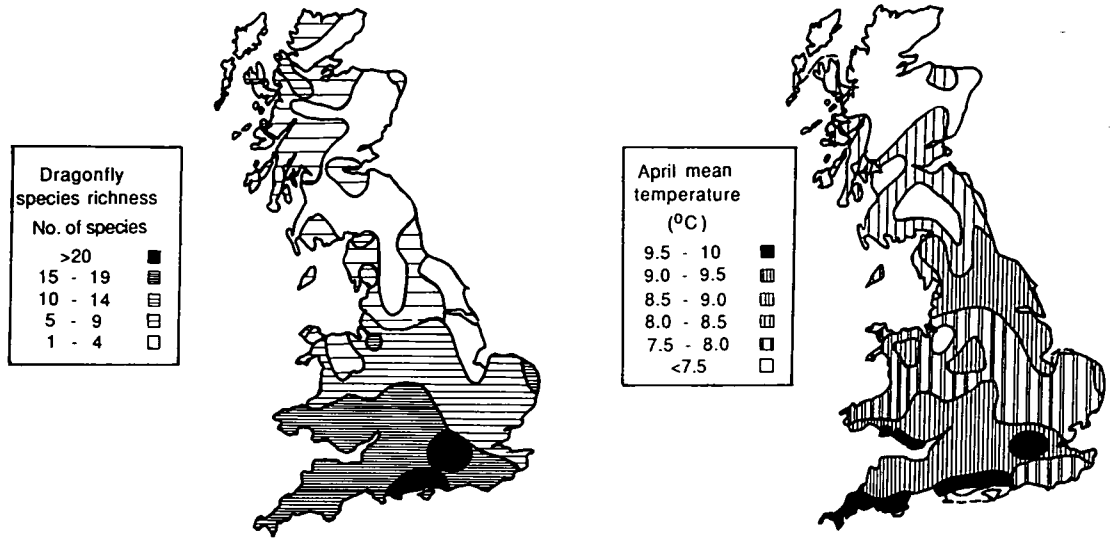

Figure 3. Numbers of species of Odonata (dragonflies) in Britain in relation to the mean temperature isotherms for April (data from the Biological Records Centre, ITE)

densities by its natural enemies. For the plant-feeding fauna of juniper (*Juniperus communis*), many of the species have distributions which are superimposed on that of the plant; they do not occur throughout its range (Ward 1977). Similarly, predators and parasitoids of insects may differ in their distribution to that of their hosts, with resulting differences in the community structure and population dynamics of those hosts.

Other limitations to invertebrate species ranges have been superimposed on climatic factors, usually agriculture and urbanisation, which reduce the ranges and extents of the natural habitats and host plants (eg juniper, Ward 1981). Continuous habitat is often fragmented into island sites. Many butterflies are thought to be affected by habitat reduction and management changes, and their ranges artificially constricted far short of their climatic limitations. For example, the silver-studded blue (*Plebejus argus*) on heaths and the large blue (*Maculinea arion*) associated with the ant, *Myrmica sabuleti*, in short grassland (Thomas 1990). Beirne (1955) related known historical changes in the ranges of some butterflies to changes in agriculture.

7.2.1 Future change

Given that a 1°C rise in temperature is roughly equivalent to a move 200 km northwards or 140 m in altitude, we can expect both an increase in population and a spread northwards of the British invertebrate fauna following climatic warming. However, the change is likely to be erratic and is hard to predict. Relict sites where species occur outside the areas in which they are common may be important in this northerly spread. Some species may start to exhibit southern range boundaries in Britain, although they do not do so at present. More species, including pests of crops, will invade Britain from continental Europe.

Those few species which have the southern boundary of their ranges in northern areas will become endangered, eg sawflies living on northern species of willow (*Salix* spp.) and northern species of juniper fauna. Montane species are at particular risk, because their move to higher altitudes may not be matched by the extent of their montane habitats (Peters & Darling 1985). Only a few montane species survive in Snowdonia now, while the Cairngorm Mountains have our highest numbers of rare arctic-alpine species of many groups, eg spiders and beetles, which are likely to become extinct. In fact, rare species of all invertebrate types will probably be at risk, because they are so vulnerable to changes in their local floras and habitats.

The change in distribution of species will be greatly influenced by the availability of suitable habitat, any barriers to movement, and the dispersal powers of the species. The current fragmentation of habitat is likely to be significant in slowing changes in distribution. Within southern Britain, many species of conservation interest are virtually restricted to nature reserves or Sites of Special Scientific Interest, and the present intensively farmed areas or urban developments between such sites may be insuperable barriers to movement. The black hairstreak butterfly (*Strymonidia pruni*) was restricted to the east Midlands, but was successfully introduced to a patchwork of new highly suitable habitats in Surrey; it has taken some 36 years to spread 4 km from the original release point (Thomas 1990).

The most important natural barrier to invertebrate distribution is the North Sea and English Channel. Higgins and Riley (1980) record 54 species of breeding butterflies in mainland Britain, but across the Channel in NW France, Belgium and Holland there are 92 species. Across the Irish Sea in Ireland, there are only 25 species. Within Britain, there are other natural barriers such as the long distances between the southern heathland areas and those of the Midlands. Similarly, the amount of limestone and chalk habitat in Britain diminishes as one moves north.

Barriers to movement are less important to species that disperse long distances, particularly to

migrants which are dispersed by large-scale air movements in the upper atmosphere (McManus 1988). Aphids are a group with efficient dispersal mechanisms of this sort: there are many pest species which would easily be able to invade any suitable new areas (Wellings & Dixon 1987). Aphids are also vectors of viruses. Many Lepidoptera are migrants; some appear annually and rarely survive the winter, but, if it were warmer, many might become resident. Bretherton (1983) suggests that as many as 15% of all British Macrolepidoptera and Pyraloidea are migrant species; of these, 34 are common and often numerous, and most arrive from northern Spain.

Greenhouse warming is predicted to occur rapidly, compared with past climatic changes. Plant distributions are likely to change more slowly than faunal distributions, and some insects could be good indicators of climatic change. On the Solway coast, some fossil beetles arrived following postglacial warming while the dominant tree was still Scots pine (*Pinus sylvestris*); oak (*Quercus* spp.) and elm (*Ulmus* spp.) did not arrive for another 2000–3000 years (Crowson 1981). Genetic adaptations where species have developed local races will break down if the change is too rapid. Isolated colonies will become part of the main population, and varieties and races associated with particular areas will be lost, thus reducing the genetic diversity of species.

Within the geographical range of any species, there are often considerable differences in behaviour, morphology and physiology, which may be sensitive indicators of climatic change. The onset and termination of diapause are adaptations for winter survival in insects of temperate areas, and are mainly controlled by climate, though daylength is often important. With increasing temperatures, insects develop faster and complete more generations within one season. There are many species whose voltinism (number of generations) changes within the British Isles, and partial generations can also occur; these are very sensitive to climatic change. The British butterfly monitoring scheme has provided long-term data from 1976 to 1986 which show how numbers have changed with different climatic conditions (Pollard 1988). Similar information exists from the Rothamsted light traps for moths. The European corn borer (*Ostrinia nubilatis*) spread through the United States during 50 years, and it was possible to predict the geographical areas where the insect completed one to four generations as a function of climate (Showers 1981).

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8. Birds

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8.1 Introduction

Bird populations are in constant flux. Changes in the geographical distribution and numbers of birds are more common than stability. The chances of detecting density changes depend upon how intensely populations are monitored. Superficial monitoring over 100 years in Britain has shown that the numbers of about 70% of our breeding species have increased or decreased markedly (Lack 1954). Since then, other authors have reviewed further changes in bird populations (Parslow 1973; Murray 1979) and some have quantified them (eg Summers-Smith 1989), although it is often difficult estimate accuracy (Marquiss 1989).

Climatic change will inevitably result in population changes. Many previous range extensions of western Palaearctic bird species were attributed to climatic amelioration, either since the last glacial period (Murray 1979), or over periods of centuries (Gudmundsson 1951) or decades (Kalela 1949; Välikangas 1951). Long-term population changes probably result mainly from changes in the extent and nature of bird habitats, caused either by climatic change or human activities; for at least the last 1000 years, man rather than climate has had the greater impact on bird habitats in Britain (Flegg 1975; Fuller 1982). Moreover, man has also influenced bird populations by purposefully reducing the numbers of some species thought to be pests (Murton 1971) or by introducing (Lever 1977) or conserving (Bibby *et al.* 1989) selected species. Nonetheless, some population distribution changes may result directly from changes in weather (Svardson & Durango 1951; Williamson 1975). Climatic change could influence the balance of competition between allopatric species, and result in changes in the geographical boundaries between them (Campbell & Lack 1985). Such changes may have occurred in the boundaries between chaffinch (*Fringilla coelebs*) and brambling (*F. montifringilla*) in Finland (Järvinen & Väisänen 1979).

The main concern for the future is to predict changes in the British avifauna, given postulated changes in climate. In the short term, changes in bird populations might be expected in direct response to physical changes in the weather. In the longer term, many other factors will be involved, including changes in habitat, human attitudes and biotic influences. A first step, therefore, is to determine how bird populations in western Europe might currently be limited directly by the climate.

8.2 The direct influence of weather on population size

Compared with other types of animals, birds are well suited to resist small changes in temperature and rainfall. They are warm blooded, well insulated, relatively waterproof, and mobile. By their behaviour, they can avoid extremes, temporarily seeking shelter from adverse physical conditions or flying long distances to avoid them. They also have some independent control over their thermoregulation. For example, they can conserve heat by fluffing their body feathers, or lose heat by raising their feathers erect, or in some species by gular fluttering, or defaecating on their feet and legs. It is, thus, rare for birds to suffer immediate physical damage due to cold, heat or storm.

Birds do, however, suffer at such times because food becomes less available. Thus, the freezing of freshwater prevents piscivorous birds, such as grey herons (*Ardea cinerea*), from getting fish; deep snow covers soil litter, making foraging difficult for ground-feeders, such as robins (*Erithacus rubecula*); while hot, dry weather reduces the abundance of earthworms near the soil surface, so fewer are available for thrushes. Sparrowhawks (*Accipiter nisus*) do not normally hunt in the rain, so long spells of rainy weather restrict the availability of their songbird prey (Newton 1986a). In cold, wet weather there are fewer aerial insects for hirundines, and on at least one occasion such weather coincided with strong winds, preventing migration, so that thousands of swallows (*Hirundo rustica*) perished (Alexander 1933).

There are many documented instances where unusual and extreme weather conditions have caused the deaths of large numbers of fully grown birds, or the poor production of young, resulting in population declines (Lack 1954; Elkins 1983).

Usually, bird numbers recover rapidly from such declines, provided that weather conditions revert to normal. Extreme weather has a lasting adverse effect on bird populations only if it occurs frequently. The currently postulated changes in the British climate do not include any certain increase in the frequency of severely cold or hot weather. The climate could ameliorate, with milder winters and wetter summers. If anything, the extreme conditions that have led to large numbers of bird deaths in Britain in the past are less likely to occur in the future. Thus, we might expect that those species traditionally viewed as vulnerable to cold weather will not suffer such major overwinter declines as have occurred in the past. In the 1962–63 severe winter, populations of as many as 23 bird species were greatly reduced, about 17% of the species then resident in Britain (Dobinson & Richards 1964). However, the predicted warmer climate will not necessarily result in 17% of the British bird species becoming more abundant, or in their populations remaining more stable. Bird populations are affected by many factors, and removing one constraining factor merely brings another into play. For example, the survival of grey herons in Britain is related to temperature (North 1979). Cold weather in winter reduces the population, but warmer winters will not necessarily result in an increase above previous maxima, because some other factor, such as rainfall or fish abundance, will limit numbers, giving rise to both seasonal and annual variations.

Thus, we may speculate that, with less frequent severe weather, the populations of many species might suffer fewer temporary declines and become more often limited by habitat rather than by weather. However, this speculation would not be true for species limited by rainfall, if rainfall were to increase. In many bird species that have been studied in Britain, rainfall influences breeding success, but without affecting the size of subsequent breeding populations. In years when few young are produced, their subsequent survival is presumably enhanced in a 'compensatory' fashion (Moss, Watson & Ollason 1982), so that breeding numbers are maintained. Among birds that feed on soil invertebrates, such as various thrush species, breeding tends to be worst in drought years (Snow 1958), while in certain birds of prey breeding success is depressed by high rainfall which interferes with hunting (Newton 1986a; Mearns & Newton 1988). However, in one well-studied species, capercaillie (*Tetrao urogallus*), it is only in poor habitats that high rainfall reduces breeding success sufficiently to cause the population to decline. In 'good' habitats, the birds maintain their numbers despite high rainfall (Moss 1986, unpublished).

8.3 The direct influence of weather on geographical distribution

Evidence that climate directly limits the geographical distributions of birds comes mainly from the coincidence between weather parameters and species ranges, eg where the edge of a species distribution coincides with an isotherm or with a particular pattern of rainfall. The northern limit of the wintering range of 60% of the 148 species of land birds in North America coincides with a mid-winter temperature isotherm (Root 1988), and for 40% of the species the eastern edge of their ranges correlates well with annual precipitation. In both directions, however, species ranges coincide with habitat ranges, making it difficult to separate the influence of weather from that of habitat. No such all-embracing analysis has been done for European bird species. In western Europe, the distributions of both weather variables and habitats are less extreme and more convoluted than in North America. Moreover, bird distributions in Europe are well mapped (Harrison 1982), particularly for Britain (Sharrock 1976; Lack 1986), so a similar analysis would be possible. The objective would be to seek significant associations between bird distributions, climate and habitat so that predictions could be made about which species are likely to extend their range as climate ameliorates prior to significant changes in habitat.

Such an amelioration has already occurred in western Europe. In the 1930s and 1940s, a period of distinct warming in the Baltic region, Iceland and Greenland was accompanied by dramatic increases in the numbers of bird species breeding in these areas, as southern species extended northwards and northern ones, to a lesser extent, retreated (Horstadius 1951; Lack 1954). There seems little doubt that climate directly influenced bird populations, because the changes occurred rapidly and coincidently; the effect was most dramatic in the far north, where entirely new breeding species rapidly became abundant. The north-western seaboard of Europe did not experience the same amelioration; if anything, the weather in western Norway and Britain cooled, and changes in the avifauna were not dramatic. There may have been recent colonisation of Britain by northern birds (Murray 1979) or an increase in their abundance associated with cool weather (Nethersole-Thompson 1966, 1973), but the evidence is poor. Many of the rarer species have remained rare, and their previous status is uncertain because of changes in observer coverage in the north.

The recorded distribution and abundance of the three commonest British arctic-alpine species – ptarmigan (*Lagopus mutus*), dotterel (*Eudromias morinellus*) and snow bunting (*Plectrophenax nivalis*) – have varied with observer coverage; whenever coverage was good, more birds were found, so it has been impossible to discern reliable population trends (Watson 1965, unpublished; Watson & Rae 1987). In contrast, the decline or extinction of some southern breeding species over the past 75 years, such as the red-backed shrike (*Lanius collurio*), Kentish plover (*Charadrius*

alexandrinus), stone curlew (*Burhinus oedicnemus*), nightingale (*Luscinia megarhynchos*) and cirl bunting (*Emberiza cirlus*), is well established (Sharrock 1976). Their declines could be linked to a cooling climate, were it not for similar numbers of southern species increasing, notably great-crested grebe (*Podiceps cristatus*), collared dove (*Streptopelia decaocto*), green woodpecker (*Picus viridus*), Savi's warbler (*Locustella luscinoides*), Cetti's warbler (*Cettia cetti*), firecrest (*Regulus ignicapillus*) and black redstart (*Phoenicurus ochruros*). Without closer scrutiny of the mechanisms involved, it is uncertain how much of these distribution changes have been caused directly by climate.

The main factor influencing the weather in Britain is the North Atlantic Drift, a warm sea current, and its associated airstream, which moderates temperatures and gives high rainfall. If the future climate is even wetter, southern bird species requiring hot summers will not thrive in Britain, despite a warmer climate overall. For only three species, capercaillie (Moss 1986), red-legged partridge (*Alectoris rufa*) (Howells 1963) and tree sparrow (*Passer montanus*) (Norris 1960), is there convincing, though circumstantial, evidence that the distributions of breeding populations in Britain are currently limited by rainfall. These species may retreat south-eastwards but, as mentioned earlier, the long-term changes in habitat may be more important than the weather.

8.4 The influence of habitat changes on British birds

Ultimately, an ameliorating climate in Britain will produce dramatic changes in bird populations by affecting their habitats. Such effects may occur in three ways.

First, and probably foremost, there may be changes in land use, for example as agricultural and silvicultural policies change in response to changing yields and markets. Yields may be directly affected by climatic change in Britain, whereas market forces may be influenced by climatic change here and abroad. The bird communities associated with various farmland habitats are well documented (O'Connor & Shrubb 1986), as are those associated with the rotational stages of coniferous forests (Newton 1986b) and of some hardwood coppicing regimes (Fuller & Moreton 1987). In theory, therefore, much can be predicted from current land use patterns and changes, eg from deforestation or reafforestation. Less predictable will be the result of novel crops, or of novel mixtures. Thus, little is known of the bird communities in British vineyards, or in agroforestry plots.

Second, there may be changes in natural vegetation. These changes would have a minor effect on bird populations, except for those few species that are totally dependent upon vulnerable natural vegetation. One obvious example is the arctic-alpine community, which may or may not survive depending on specific changes affecting wind velocity and snow lie at high elevation.

The third major change in habitat will be caused by rising sea levels, and will affect the bird populations of salt marshes, mudflats and shallow inshore waters. Boorman, Goss-Custard and McGrorty (1989) considered various impacts, depending on the extent of sea level rise and whether sea defences are maintained, rebuilt or abandoned. If sea walls and the agricultural hinterland are abandoned, new coastal marshes will form and some bird life could benefit (Everett 1987, 1989). Where sea defences are maintained with higher sea walls, storm surge barriers or impermeable barriers across estuaries, there will be less coastal habitat. Particularly at risk are the large populations of wintering wildfowl and waders that currently depend on the extensive salt marshes and mudflats of British estuaries (Moser 1987).

8.5 The impact of climatic change on migrant birds

Large variations in the abundance of some breeding birds in western Europe have been linked to changing weather conditions elsewhere in the world. Annual variations in the Dutch breeding population of purple herons (*Ardea purpurea*), and in their survival rate, are closely correlated with rainfall in their wintering area in West Africa (Den Held 1981; Cavé 1983). Several species of migrant passerines suffered large population declines in 1969 following severe drought in the African Sahel zone, an area where they were known to spend part of the winter (Winstanley, Spencer & Williamson 1974). Most severely affected were sand martins (*Riparia riparia*) and whitethroats (*Sylvia communis*), whose breeding populations in Britain have still only partially recovered. To predict population changes of this sort requires knowledge of the wintering areas of British breeding birds, and of the future climate of those areas. Conversely, for birds that winter in Britain, we need to know where they breed and the future climate there. Fundamental to predictions of change in migrant bird populations is a knowledge of which areas (breeding, staging or wintering grounds) are currently limiting population sizes: a decline in wintering habitat will not necessarily affect a population already constrained by a limited breeding habitat. For some wetland species, both their tundra breeding areas (Pain 1988) and their estuarine wintering areas in Britain are likely to be substantially reduced.

8.6 The impact of climatic change on seabirds

Seabirds breeding in much of Britain are not restricted by a lack of breeding sites because the cliffs, headlands, islands and shingle spits where they breed are usually plentiful, and rises in sea level will affect them only slightly (Boorman *et al.* 1989). In contrast, their food supply – small fish species such as sandeels (*Ammodytes* spp.), sprat (*Sprattus sprattus*) and young herring (*Clupea harengus*) – are known to be affected by sea temperature and currents, as well as by commercial fishing activities. A recent decline in the availability of sandeels around the Shetland Islands has been accompanied by drastic breeding failures in some seabird populations.

Both phenomena have coincided with a recovery in local herring stocks, and a marked increase in seawater temperatures, as a greater influx of warm North Atlantic water has entered the northern North Sea. Some authors place emphasis on local industrial sandeel fishing as the probable cause of seabird breeding failure (Avery & Green 1989), but fisheries data suggest that 'natural' factors, such as the increases in herring stocks or sea temperatures, are just as plausible (Kunzlik 1989). The influence of natural factors now seems the more likely explanation, because the poor breeding performance of seabirds has occurred in areas well away from industrial sandeel fishing, and is correlated with increased sea temperature, amongst other environmental changes (Harris & Wanless 1990). As yet, the influence of changing climate on seabirds cannot be predicted because insufficient is known about the interrelationships between seabird populations, their food supply, commercial fisheries, and the sea 'climate'.

8.7 Conclusions

Despite some knowledge of the effects of weather on bird populations, it is difficult to predict avifaunal changes following climatic change in Britain. This difficulty exists for several reasons.

i. Bird populations are in constant flux.

ii. Birds are robust organisms, resistant to small or temporary changes in weather so, although their populations are ultimately influenced by climate, the main proximal factors affecting most British birds are probably habitat and associated food supply.

iii. Within the historical record of avifaunal changes in western Europe, it is difficult in most regions to disentangle small effects of climatic change from the large effects of man-induced habitat changes. This difficulty applies particularly to Britain, which has not experienced pronounced climatic change in the last 100 years.

iv. The current scenarios for climatic change in Britain are uncertain, and predictions of changes in habitat are necessarily speculative.

v. Changes in climate elsewhere in the world will have a large influence on the populations of our migrants, and on future land use policies in Britain.

Nevertheless, it is anticipated that predictions of avifaunal change may be attempted and, towards this end, three areas of study should prove fruitful. First, an analysis is required of the distributions of European bird species, to search for coincidence with existing patterns of climate. Second, an analysis is needed of ringed bird recoveries, to determine the breeding, staging and wintering grounds of British migrant species. Third, an examination is required of Common Bird Census changes (Marchant & Whittington 1988) in relation to weather, to detect the relative sensitivity of different species.

It seems unlikely that there will be unprecedented large changes in the near future. The effects of climatic change in Britain are likely to be small at first, but will accelerate as land use changes affect major bird habitats. It is predicted that climatic changes elsewhere in the world will be more extreme and more rapid than in Britain, so large changes in the populations of migrant species may occur well in advance of changes in resident species.

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9. Mammals

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9.1 Introduction

This Chapter discusses some of the effects of variation in climate on the ecology of British mammals, with predictions of future changes in distribution through the British Isles. Two detailed case studies of present-day climatic influences on mammals are given as examples, and suggestions are made for research needed to understand and predict the effects of climate.

Obviously, global warming will influence the fauna through many second and third order effects, as well as directly through temperature. Changes in precipitation are expected, as well as changes in agriculture, forestry and other aspects of land management, with many of these developments being probably much more important to various species of mammal than the actual variation in temperature. As the direction of these changes and the effects of interaction between them cannot as yet be predicted, this Chapter concentrates mostly on the direct effects of changes in temperature.

There are two characteristics of mammals which set them apart from many other animals in their mechanisms of dealing with differences in environmental temperature.

i. They are endotherms; therefore, body temperature is independent of that of the environment: more or less constant in most, or regulated as in the hibernators (eg hedgehogs (*Erinaceus europaeus*), dormice (*Glis glis* and *Muscardinus avellanarius*)). There are various, very effective mechanisms of thermo-insulation.

ii. Mammals (except bats and marine mammals) are not very mobile, compared with the other endotherms, ie birds; if climatic conditions change in an 'island' situation, mammals would probably be less able to respond by immigration or emigration.

9.2 Distribution of mammals in the British Isles

All mammal species occurring in Britain also have an extensive distribution on the continent, over a wide range of latitudes (Corbett 1980), which suggests that each species has a wide tolerance to variation in climate. In some cases, this tolerance is genetically determined, with different morphs occurring in different climatic situations. For instance, in red squirrels (*Sciurus vulgaris*) it has been shown that there is a balanced polymorphism for colour patterns with latitude in Europe (Voipio 1969), with one subspecies (*leucourus*) endemic in Britain. In general, it seems likely, however, that the large latitudinal range of a species indicates the ability of individual animals to adapt to different environmental temperatures.

Of the 52 species of wild mammals occurring in mainland Britain (of which 14 were introduced), 19 have a northern limit somewhere on the British Isles. Twelve of these are bats, and, of the other seven, five are introduced species (such as grey squirrel (*Sciurus carolinensis*), muntjac deer (*Muntiacus reevesi*) and fat dormouse (*Glis glis*)). One mammal, the mountain hare (*Lepus timidus*), occurs only in the northern part of the UK for what are probably climatological reasons: wildcat (*Felis silvestris*) and pine marten (*Martes martes*) are also northern species, but probably only because of persecution in the south (Corbett & Southern 1977; Corbett 1980).

It seems probable that populations of those species which are at the edge of their distribution in Britain will be most affected by the predicted changes in climate, with 'southern' species expanding northwards, and the mountain hare retreating. Similarly, it may be expected that 'southern' species will expand to greater altitudes where possible, and that the mountain hare will similarly retreat, or disappear from some hills. Thus, if climatic change were a matter of increase in temperature alone, many mammals, especially bats, would increase their range in Britain, and perhaps some species of bat would expand their present range from the continent to Britain.

However, changes in rainfall and land use have not been taken into

account in these predictions, and their effects may well override any temperature-related changes.

9.3 Examples of effects of climate on populations of individual species

9.3.1 Red deer (Cervus elaphus)

The ecology of red deer has been studied more intensively than that of almost any other mammal in Britain, and many effects of climate on populations have been demonstrated. For instance, Clutton-Brock and Albon (1989) showed for the island of Rhum, on the Scottish west coast, that there is a good correlation between minimum temperatures during early winter and subsequent adult mortality. Temperatures during the period December–February were inversely correlated with calving rates, and April–May temperatures correlated with subsequent birth weights. There were also many separate effects of precipitation: rainfall in June correlated with calf mortality in summer, rainfall during late summer correlated with subsequent adult mortality, while rainfall in September correlated with calving rates, calving dates, calf mortality in winter, and yearling mortality.

Red deer in the central and eastern Highlands of Scotland appear to be affected by climate in a different way. For instance, Watson (1971) demonstrated that the number of days with snow lying correlated closely with winter mortality of adults, with calf mortality, and with subsequent birth rates. However, calf birth weights were uncorrelated with any index of winter severity, except for mean daily temperature in March (Albon 1983, in Clutton-Brock & Albon 1989).

Even from this one sample of correlations, it will be obvious that the effects of climatic change on red deer populations in Britain will be highly varied, and it is impossible to make national predictions despite our relatively good knowledge of the species. It is likely that the effects on most other species of mammal will be similarly complex.

9.3.2 Otter (Lutra lutra)

Because this species spends a considerable part of its time in water, which is a highly thermo-conductive environment compared with air, it is likely to be more affected by changes in environmental temperature than most other similar-sized mammals. Preliminary results of studies at ITE's Banchory Research Station, using temperature-sensitive radiotransmitters on free-living otters, suggest that the core temperature of the body may fall as much as 2°C during foraging bouts in water of 6–8°C (P Taylor, pers. comm.). In these circumstances, it is predicted that considerable extra energy is needed simply to restore the body temperature. Consequently, increases in water temperature are likely to result in lower energy requirements, ie a need for fewer prey per day. As prey populations may have considerable effects on otter reproduction and mortality (Kruuk, Conroy & Moorhouse 1987), different energetic requirements of the predator could possibly be reflected in increased population densities.

In addition, in populations of salmonids, which are very important prey species (Jenkins, Walker & McCowan 1979), productivity in captivity improves with temperature to an optimum, which tends to be in the region of 10–15°C (after which it drops sharply; Elliott 1982). Consequently, it has been shown that small artificial increases in water temperature of Scottish rivers are correlated with productivity of the new prey populations (Morrison 1989). In general, increases in environmental temperature are likely to be beneficial to otter populations in Britain, whilst changes in precipitation are likely to have little effect on this species.

9.4 Further research

It is important that changes in the distribution of mammals in Britain, including changes in altitudinal distribution, are monitored, and causal factors identified. Key species should be those which appear to be at the edge of their range for climatological reasons, eg several bats, and the mountain hare.

There is a considerable gap in our knowledge of the direct effects of environmental temperature on energy expenditure in mammals. Such knowledge will be important in order to understand the effects of climatic change, and one project has been started in ITE to study this problem in otters. Similar research should be carried out on mountain hares and bats, using radiotelemetry on animals in their natural environment.

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10. Plant communities

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10.1 Introduction

If current forecasts of climatic change are accurate, then there will be significant effects on the structure and species composition of many natural and semi-natural plant communities within the next 100–150 years. Clearly, these changes must be identified before they occur (prediction), or as they occur (measurement). Studies have begun in ITE to identify the possible areas where change is most likely to be detected. This work has highlighted some of the difficulties in detecting change *per se* and the subsequent problems in determining cause/effect relationships.

10.2 Change: where will it be most easily detected?

Basically, for the purposes of monitoring the effects of climate on vegetation, change can be classified into three main groups: (i) where the mean regional climate has a direct effect on species, (ii) where climatic extremes affect vegetation change through disturbance, and (iii) where the climate exerts an indirect effect through other ecosystem processes, such as increasing net primary production, modifying competitive interactions between species, or accelerating succession.

10.2.1 Direct effects on species

Vegetation change will involve either the colonisation of new species typical of warmer climates, or the extinction of species typical of colder climates. It is difficult to predict which species are likely to be the best indicators of climatic change, because distribution maps show a plethora of species whose British distribution is apparently limited by some aspect of climate (Perring & Walters 1962). However, there are three broad groups of species which are likely candidates for initial study:

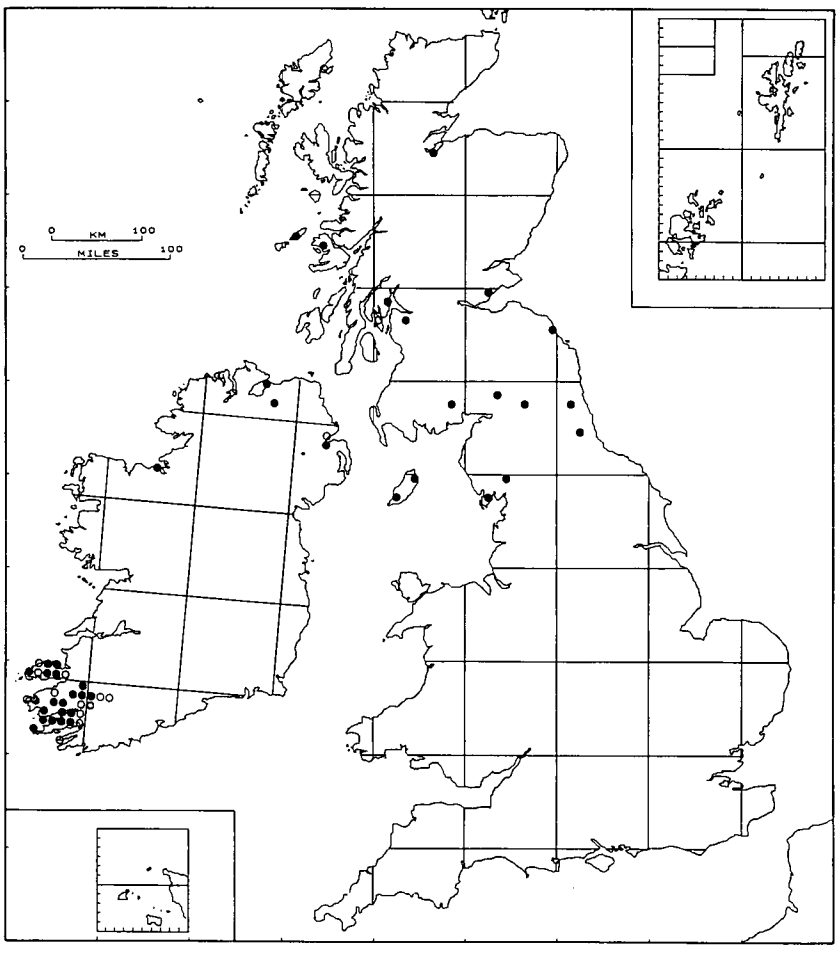
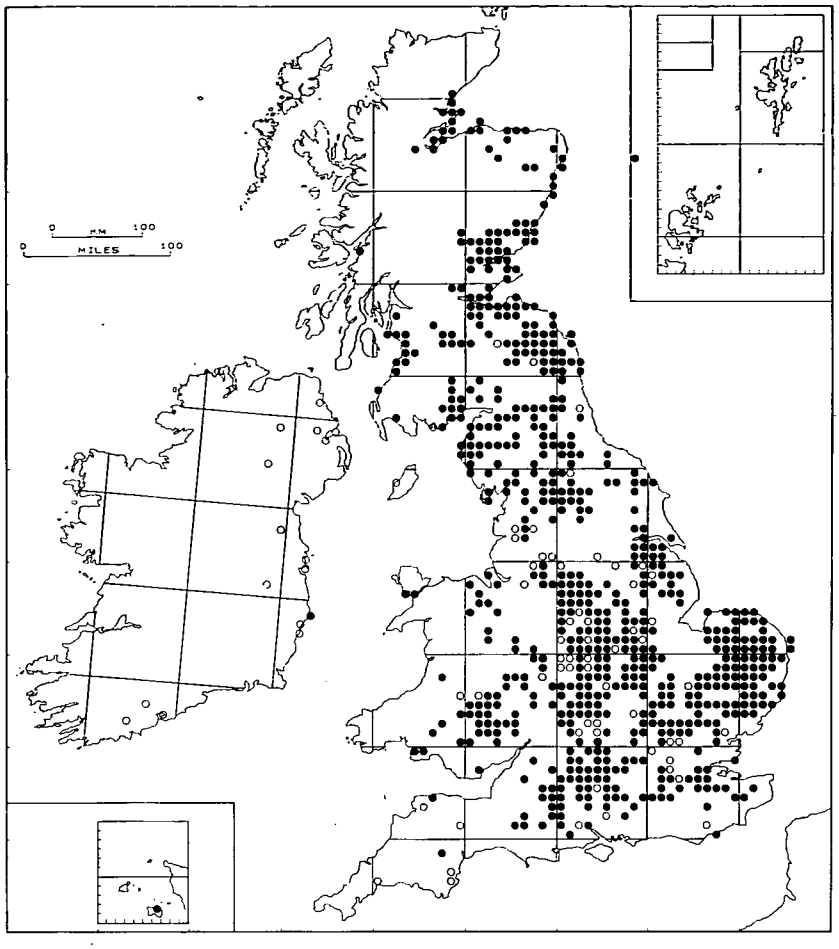
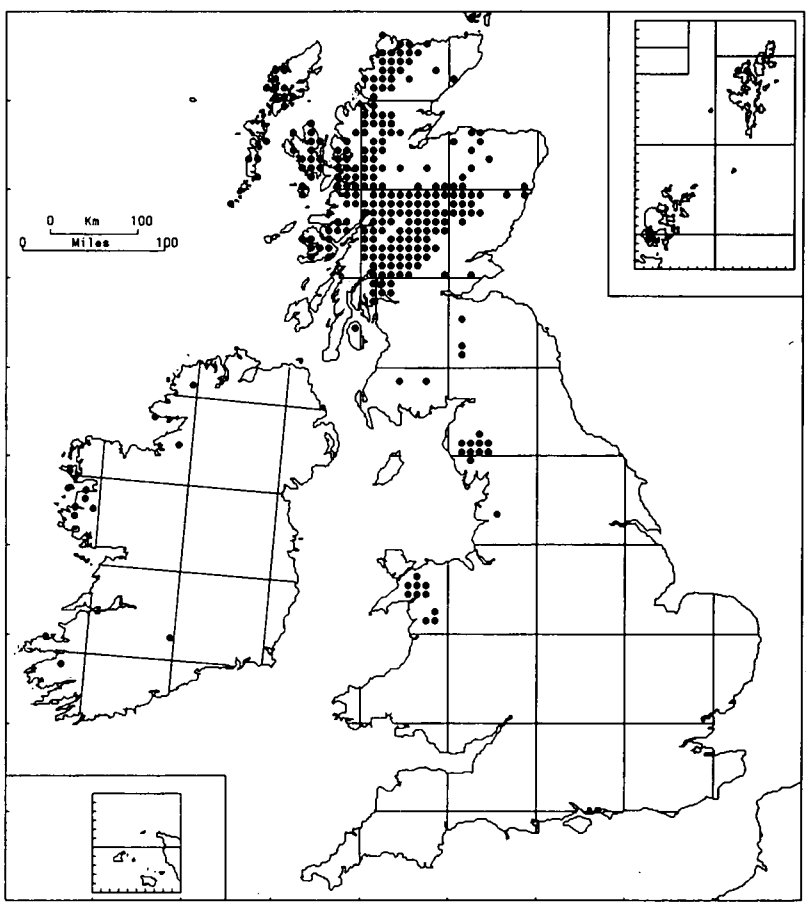


Figure 1. The current distribution of three saxifrages from the data base held in the ITE Biological Records Centre. These species would be ideal candidates for studying response to changing climate, because of their contrasting distributions:
i. kidney saxifrage (*Saxifraga hirsuta*) – a Lusitanian distribution,



ii. meadow saxifrage (*Saxifraga granulata*) – a widely distributed species



iii. yellow mountain saxifrage (*Saxifraga aizoides*) – a montane/northern species

the Lusitanian flora, alien species with a southern distribution, and the arctic-alpine flora.

Lusitanian species, such as the Dorset and Cornish heaths (*Erica ciliaris* and *E. vagans*) reach their northern limits in the south-west of England and/or western Ireland, and may expand their British range if the climate becomes warmer and wetter. Introduced alien species from warmer climates, such as the holm oak (*Quercus ilex*) and the Hottentot fig (*Carpobrotus edulis*), are already established in the south-west of Britain, and are obvious candidates for study. Arctic-alpine species, on the other hand, are found mainly in montane areas, where the climate is harsh, and the British distribution of these species is likely to contract if the climate becomes warmer, with the possible extinction of some species.

An example of one group of plants that could be considered for further study is the saxifrages (*Saxifraga* spp.), because of their current British distributions. They include:

i. Lusitanian species: the kidney saxifrage and St Patrick's cabbage (*Saxifraga hirsuta*, *S. spathularis*),

ii. widely distributed/lowland species: meadow and rue-leaved saxifrage (*S. granulata*, *S. tridactylites*), and

iii. arctic-alpine/montane species: starry, mossy, yellow mountain and purple saxifrage (*S. stellaris*, *S. hypnoides*, *S. aizoides*, *S. oppositifolia*).

The distribution of one member from each of these groups shows the clearcut nature of the distributions, and there is obvious potential for mapping their spread as climate changes (Figure 1). Although it may be possible to predict the likely change in distribution of the Lusitanian and arctic-alpine species in response to climatic change, it is much more difficult to forecast what might happen to *S. granulata* or *S. tridactylites*.

Gross change in these species may be detected by mapping their distributions at regular intervals, as is done within the Biological Records

Centre (BRC) at ITE Monks Wood. However, accurate assessments of the effects of climatic change will require detailed autecological studies of existing populations, so that range expansion and contraction can be measured. For example, a detailed baseline study of the Dorset heath, a Lusitanian species, and its hybrid with the cross-leaved heath (*Erica tetralix*), a widely distributed species, has already been established, and has indicated that these species are expanding their ranges (Chapman 1975).

An important point to be made about the potential impact of a warmer climate in allowing southern species to spread northwards is that the major limiting factors may not be climatic. Migration speed northwards may be controlled by the efficiency of dispersal, and the amounts of suitable habitat available for colonisation. As there has been a massive loss of semi-natural habitats, especially in lowland Britain, over the last few centuries, northward migration may be extremely slow.

10.2.2 Effects of extreme events

When extreme climatic events occur, there is often catastrophic death of individuals and populations. Recent examples in Britain include the October gales of 1987 affecting the southern woodlands, the hot dry summer of 1976 affecting heathlands, directly through heather (*Calluna vulgaris*) death (Marrs 1986), and indirectly through increased 'accidental' fires, and perhaps the dry summer of 1989. The important feature of such catastrophes is that they initiate change, and the community regenerates, either cyclically to replace the original community (cyclic regeneration), or by the invasion of new species. Good examples of such change occur in Breckland where heather death started in 1976 during the hot summer, and increased in the following two to three years after outbreaks of insect herbivores. In the affected area, there was immediate large-scale invasion by birch (*Betula* spp.) (Marrs 1986), and hence succession away from heathland towards woodland. Such data emphasise the importance of catastrophes in initiating new successions. Where new species are migrating northwards, successful colonisation could be accelerated if the propagules arrive after disturbance events. Effectively, disturbance could act as the major factor controlling the northwards spread of species; alternatively, it might hasten the demise of others.

There may also be complex interactions, with increased disturbance after extreme hot dry years allowing the spread of southern species, but rapid contraction after a single year of severe frost. With its fluctuating climate, Britain may be ideal for monitoring these interactions.

Studies of patch dynamics in sensitive communities, where the normal periodicity and return interval of such catastrophes is known, may help to detect important influences of climate (White & Pickett 1979). Moreover, this type of catastrophic disturbance may be an important factor allowing bursts of invasion by species typical of warmer habitats. As information is already available on the Breckland heaths, a southern habitat with a continental climate (by British standards), and the cycles are not too long (15 years), these heaths are likely 'pressure point' communities. Baseline monitoring and extensive study of community dynamics are currently in progress.

10.2.3 Indirect effects through ecosystem processes

Other vegetation changes are likely to be much more subtle than those described above, when the same species may persist, but be markedly altered in relative abundance. As the productivity of most ecosystems is likely to increase, because of higher temperatures, higher or modified rainfall, at least in some areas, and higher CO_2 concentrations, an approximation can be obtained of the likely effects of increased vegetation growth, using experiments where other growth-limiting factors are alleviated, as a model. Fertiliser addition is often used to increase vegetation productivity, and, when applied to semi-natural communities at high rates (agricultural rates), the growth of aggressive productive species has been promoted at the expense of subordinate ones. However, recent research in Europe suggests that, even where much lower amounts of nutrients are added in polluted rain, similar effects occur, with increasing dominance of competitive grasses on infertile heathlands and chalk grasslands (Heil & Diemont 1983; Bobbink & Willems 1987), and a dramatic loss of bryophytes and lichens (During & Willems 1986). Thus, if climate does tend to increase the productivity of natural and semi-natural vegetation, then some competitive species are likely to flourish, but at the expense of the understorey species, and especially the lower plants.

10.3 Problems in detecting vegetation change

There are two fundamental problems in detecting vegetation change: first, the separation of significant directional change (ie the signal) from background fluctuations (noise), and, second, the identification of cause/effect relationships. These two problems are illustrated using real data collected in a long-term monitoring scheme at Moor House International Biosphere Reserve, an upland reserve which is likely to be vulnerable to climatic change. The data presented here are from one experiment (heath rush (*Juncus squarrosus*) grassland experiment) in a set of ten established between 1954 and 1972 by the Nature Conservancy, and continued first by NCC, and, since 1982, by ITE (Marrs *et al.* 1986). The experiments were set up to cover the range of upland vegetation found on the Reserve, and, in each experiment, the effects of sheep grazing versus no sheep grazing are compared. At one blanket bog site, a rotational burning sequence is also included. The general aim of the study is to measure vegetation change, and to identify important signals (ie changes induced by management) from background noise (species fluctuations in abundance that are not accounted for by known events).

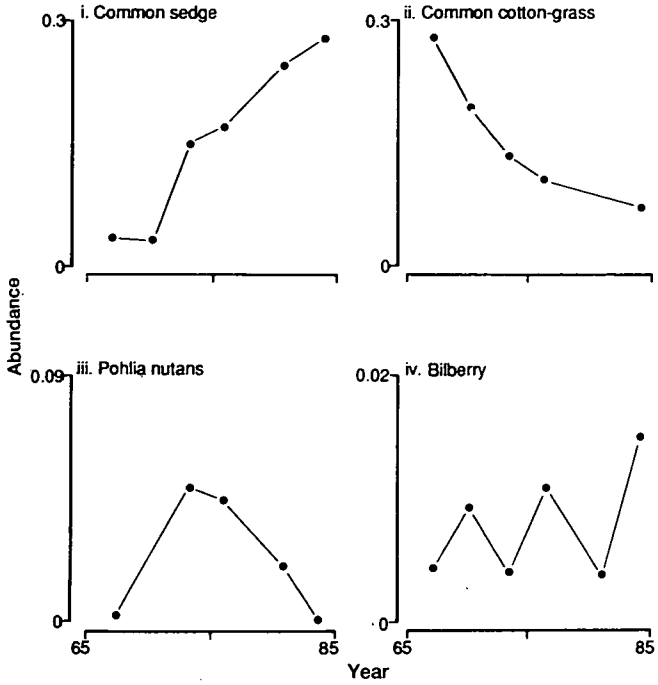


Figure 2. Observed change in abundance of four species in the heath rush grassland experiment at Moor House International Biosphere Reserve between 1965 and 1985, showing examples of directional change (i, ii) and fluctuations/noise (iii, iv)

10.4 Separation of signal from noise

In the heath rush grassland experiment, four typical examples of species response through time are shown in Figure 2. Obviously, common sedge (*Carex nigra*) was increasing and common cotton-grass (*Eriophorum angustifolium*) was decreasing, but *Pohlia nutans* showed a curvilinear response and bilberry (*Vaccinium myrtillus*) was erratic. Clearly, the first two species are showing a consistent directional change over the period examined, but the latter two must be viewed as noise. Where such noise occurs, it is impossible to measure change in abundance from a few points (Figure 3), and, moreover, long-term data are essential even to determine that they are noisy. Thus, the current classification of common sedge and cotton-grass within this experiment may prove erroneous when data for a longer period become available.

It is possible to use multivariate ordinations for data from all species to assess change, and comparisons can be made between sites (Figure 4). In this example, the grazed versus ungrazed plots are changing in both treatments in the same direction, but at different rates; the enclosed plots are changing towards blanket bog much faster. Rates of change on the ordination axes may provide a useful, albeit crude, method for assessing climatic change impacts.

10.5 Cause/effect relationships

It is impossible to separate cause/effect relationships without detailed experiments where the causal factors of interest are manipulated. For example, the results shown in Figure 4 show that both grazed and ungrazed heath rush grassland changed towards blanket bog between 1966 and 1984, but the trend was faster when grazing was removed. However, directional change in other unknown environmental factors may also have occurred during this period, and these covariates with time complicate the interpretation of cause/effect relationships. Thus, the general trend in the grazed plots towards blanket bog could be the result of:

- unknown vagaries of the climate, eg individual extreme events, some periods favouring certain species at the expense of others;
- a possible increase in nutrient inputs, particularly nitrogen, through rainfall deposition and cloud capture;
- possible slight reductions in grazing pressure on the grazed site, through changes in stocking density or animal preferences;
- changes in unknown variables.

What has been determined is that this background change is slower if sheep grazing is continued.

Clearly, the best way of separating cause/effect relationships is by conducting experiments in which the causal factors are manipulated. However, it may be possible to obtain pointers using the newer

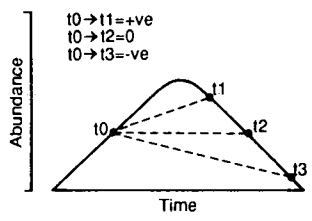


Figure 3. Hypothetical diagram illustrating the problem of detecting change when there are few sampling points and change is curvilinear. Opposite results are obtained, depending on the time interval between sampling points

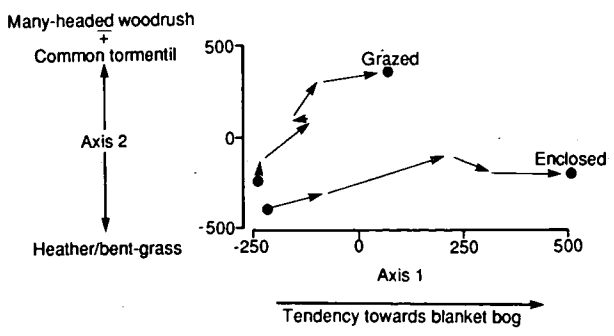


Figure 4. Trajectories through time for the sheep-grazed and enclosed (ungrazed) plots of the heath rush grassland experiment at Moor House International Biosphere Reserve between 1965 and 1985, using multivariate analysis

methods of multivariate analysis (Ter Braak 1987), where community trends can be related to measured environmental variables. To be successful, this approach requires measurements of the environmental factors of interest throughout the study period.

So far, the difficulties in demonstrating that vegetation change has been caused by changes in major driving variables have been considered. However, change can also be initiated by secondary effects that may be promoted by climatic change or its interaction with other major driving variables, such as pollution and grazing pressure. Secondary effects that might occur are the increased productivity of dominant species, and hence a lower resource availability (light and nutrients) for subordinate species, or responses induced by changed invertebrate herbivory.

10.6 Conclusions

Although it is possible to detect the effects of climatic change for certain 'pressure point' communities where species may be gained or lost, for most communities separation of signal from noise and the isolation of causal factors are likely to be major problems. In order to detect the subtle effects of climatic change on vegetation, an expanded system of long-term site monitoring must be set up, and linked intimately to (i) experimental studies of comparative plant ecophysiology, including the competitive relationships between species under various management scenarios, and (ii) simulation modelling.

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11. Coastal habitats

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11.1 Introduction

One of the dramatic consequences that can be expected from global warming is a rise in mean sea level. The consensus of opinion is that, over the past century, mean sea level has risen by some 10–15 cm (Robin 1986), although in many parts of the world this rise is obscured by vertical land movements (Pirazzoli 1986). The rising temperatures affect the sea level in several different ways; these include the direct thermal expansion of the oceans, the melting of glacier ice, and the melting of polar ice sheets. Only the first-mentioned process, the thermal expansion of the oceans, has been modelled effectively, and opinions differ as to the relative significance of the various processes contributing to the sea level rise. The subject of sea level rise and the British coast has been treated more fully elsewhere (Boorman, Goss-Custard & McGrorty 1989).

11.2 Sea level rise

The net result is a wide variation in the forecasts of sea level changes over the next century or so. Estimates vary from 0.5 m up to an extreme of 3.5 m (Hoffman 1984). A recent Dutch study postulates a probable rise of 1 m in the next 100 years and a possible rise of 5 m in 200 years (Anon 1986). Similar or even higher predictions have also been made for this country (a rise of up to 4.5 m in less than 150 years has been predicted for the Wash – T Shennan, pers. comm.). Something approaching a consensus view was provided by Robin (1986), with a middle estimate of 0.80 m and a maximum of 1.65 m. More recently, estimates have been revised downward to an estimated rise of 300 mm by 2050, with extremes between 70 mm and 620 mm (G Alcock, pers. comm.). The Dutch Rijkswaterstaat is using a figure of 600 mm by 2090 for planning sea defence in the Netherlands (Anon 1989).

The general, eustatic, rise in sea level is not the whole story. In Britain, the areas of coast most susceptible to rises in sea level lie in the south-east where the land is sinking relative to the sea. Estimates of this sinking vary, but it could be in the order of 3 mm per year (Butler 1978). Second, climatic changes themselves would have a direct effect on at least some of the species, communities and ecosystems on the coast. Finally, a recent report has suggested that the north-east Atlantic has become notably rougher over the past 25 years (Carter & Draper 1988), which would significantly increase the impact of a rise in sea level, especially on exposed coasts.

Sea level is not a constant factor, but is subject to complex cyclic (tidal) and non-cyclic fluctuations (eg changes due to variations in barometric pressure, changes due to wind, ie storm surges, etc). The changes in tidal range (difference in level between mean high water spring tides and mean low water spring tides) around Britain vary from as little as 2 m in open water and along the east Norfolk coast up to 11 m and over in semi-enclosed areas such as the Severn estuary. In such areas, the tidal range increases up the estuary to a maximum, after which the tidal influence progressively decreases, although some effects can still be detected at very considerable distances from the sea.

The effect of a rise in sea level on the tidal regimes is not a simple one, as the various components that make up the tide are affected differently. While a first approximation can be made by simply adding the sea level rise, as a constant, to the tidal curves, recent studies in the Bay of Bengal (Flather & Khandker 1990) have shown the need for models to define the changes accurately. These studies showed that tidal amplitude and storm surges could be both increased and decreased at different points in an estuary following a rise in sea level. The magnitude was relatively small, but by no means insignificant (tidal amplitude +6% to −8%, tide + surge elevation +12% to −25%). However, these results are from a preliminary study of one particular site, and can only be taken as indicating the need for detailed studies of specific cases.

A factor omitted in the Bengal study was the influence of river flow. The

scenario for Britain includes the possibility of an increase in rainfall of 20%. Such an increase could clearly affect river discharge, which, if coincident with tidal or surge flooding, could have important consequences.

11.3 The British coast

The coastline of Britain can be subdivided into two categories, the mainly low-lying soft coasts, often protected by a sea wall, and the harder, predominantly cliff, coasts. The cliff coasts associated with harder rocks in the north and west would be little affected, even with a sea level rise of some magnitude, although, even on these predominantly rugged coasts, there are sheltered inlets with salt marsh, shingle and sand dune communities. However, in the absence of artificial restraints, these isolated communities and ecosystems would probably adjust to rising sea levels by slowly migrating landwards. Difficulties could arise if these natural changes came into conflict with man-made structures or agricultural activities.

11.3.1 The effects of sea level rise on coasts

A rise in sea level would result in increased erosion, but this can usually release enough sediments into circulation to allow the coast to reform more or less unchanged, the classic 'sea level transgression'. These processes are illustrated by the barrier island coasts found in north Norfolk or, especially, the north of the Netherlands and north Germany. The development of new marshes and mudflats is, however, a slow process, and it is possible that the rate of sea level rise might be too great for these natural processes of recovery to take place. In addition, these processes depend on there being no artificial barriers to limit the advance of the sea landwards, and no human use of the dunes to restrain the natural dynamic processes.

Along nearly all of the low-lying coasts of Britain, these natural processes are inhibited by the existence of sea walls that protect life and property against any intrusion of the sea. A rise in sea level would increase the rate of erosion of marshes seawards of the sea wall and the sediment would be lost from the immediate system. However, most of the sea walls are composed of erodable material and are lightly protected against erosion. They are generally only high enough to give protection against present sea levels. A sea level rise of the magnitude postulated would require a major review of sea defence and coast protection policies. The effect of sea level rise on coastal ecosystems would thus depend considerably on the choice of options for sea defence and their implications. Only then can consideration be given to the effect of sea level rise on the vegetation of mudflats and salt marshes, on the populations of the invertebrates of the mudflats, and on the bird populations associated with these habitats.

Some parts of the low-lying coasts are fronted and protected by sand dunes or shingle banks. These areas would be vulnerable to change as a result of a rise in sea level, especially where there is insufficient space for them to reform landwards, or where human use of the dunes means that natural dynamic processes have to be restrained.

Sea level rise would also present a significant problem in those areas with a cliff coast where the cliffs were composed of softer rocks, such as the 'earth' cliffs of north Humberside and parts of Norfolk and Suffolk. The present, not inconsiderable, rates of erosion would be dramatically enhanced. If erosion was allowed to proceed unchecked, then there would be a substantial enhancement of the supplies of sediment to salt marsh and sand dune areas further along the coast. Conversely, the prevention of erosion would cut off this supply of sand and sediment, and could result in increased erosion elsewhere.

In addition to the direct effect already mentioned, a rise in sea level would have its effects some distance inland. There is likely to be increased flooding in coastal areas by sea- or brackish water, and salt penetration of the groundwater would increase further inland (Salinas, Delaune & Patrick 1986). There would be a more marked and more frequent penetration of salt water upstream, such as occurred in the Norfolk Broads in March 1988 with the dramatic fish kill. There could also be effects far inland as a result of new sea defence strategies.

11.4 Socio-economic considerations

There are already many conflicting demands on our coastal resources. These include the needs of sea defence, industrial developments, amenity and recreation, and nature conservation.

Along undefended coasts, the natural compensatory movements of coastal deposits and their associated ecosystems will introduce new conflicts of land use. Along shorelines protected by sea walls, present conflicts will be greatly increased as the shorelines are narrowed or destroyed. New sea defence options will each have their own environmental problems. Relocation of the sea wall landwards will invariably cause a range of socio-economic problems, as this approach will affect not only agricultural land but also residential areas. The building of major estuarine barriers, as well as being very expensive, will create new habitats but also new problems.

However, there are yet further complications. A warmer climate will encourage all forms of coastal recreation. These extra demands will be particularly difficult to meet at a time when decreasing coastal resources are coming under increasing pressures from all sides.

The best that we can do is, first, to predict as accurately as we can what the changes will be, and, then, to formulate plans to ensure that optimum use is made of our coastal resources, including the design of new techniques for their integrated management.

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12. Historical evidence of climatic change effects

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12.1 Introduction

For the past 25 years, the description of the English race as obsessed with changes in the weather might more accurately be phrased as obsessed with change in the climate. The weather in the years from 1945 to 1964 was so poor that from 1965 to 1980 we worried about the onset of another ice age. For example, Parry (1978) wrote 'Decadal averages of both winter and summer temperatures reached a peak from 1940 to 1950 and have since declined. Indeed the indications are of a present trend in cooling on a hemispherical scale from the Yukon to Iceland with increased pack ice in the sub-Arctic and reduced sea temperatures in the North Atlantic'. By 1980, we had begun to worry about the reverse. Now it seems generally agreed that rises in average temperature must be expected as a result of the increase in greenhouse gases. Various scenarios have been proposed for the next few decades; broadly speaking, a rise in temperature of 2°C, together with possibly higher rainfall, perhaps wetter in winter and drier in summer, over the next 50 years might be accepted by most as a reasonable prediction. What effects will these changes have? Some are clear, though not accurately quantifiable: the sea level will rise because of expansion and perhaps some ice melting; some are much less clear. The effects on plants and animals seem most obscure. On the one hand, we are told to expect a climate in southern England similar to that in southern France today, but we are not told to expect cork oak (*Quercus suber*) forests or maquis and garrique. Instead, the ecologists bewail the impossibility of doing large-scale experiments on communities of many species simultaneously to assess competitive interaction, because using 'open top' and 'growth' chambers for investigating the responses of species, one at a time, gives only a limited perspective.

Nature has, however, been carrying out the experiment over millenia, and, for Britain, the results of the last 1000 years have been recorded, albeit in a scattered and haphazard fashion, in the historical record.

12.2 The change in climate

The evidence, as compiled by Lamb (1965), suggests the 50 year average of 900 AD be estimated as 9.25°C, rising over the centuries to 10.25°C in 1175 to 1300 AD, then falling to 8.75°C in 1575–1675, before rising again to 9.5°C in the first half of the present century. Thus, there would appear to have been two epochs deviating from the norm: a warm period from, say, 1100 to 1550 AD and a cold one from 1550 to 1800 AD, the mediaeval warm period and the little ice age respectively.

Climatic changes may range from short-term fluctuations, lasting a few years, to those extending over thousands of years. The so-called little ice age was an example of such a fluctuation, or a number of fluctuations, lasting a few centuries. It began in the 13th and 14th centuries, and, after an interval of more clement conditions, culminated between the mid-16th and mid-19th centuries. The lower temperatures experienced over most, if not all, of the globe affected plant growth and agriculture, particularly in the higher latitudes and at high altitudes where conditions were naturally most marginal (Grove 1988).

For several centuries before the little ice age, climatic conditions in Europe had been kind. There were few poor harvests. Grain was grown in Iceland and Greenland. The northern fisheries flourished, and productive vineyards thrived in mainland Europe 500 km north of their present limits. There are indications that sea level around parts of the North Atlantic during the 13th century may have been 50 cm higher than in 700 AD. By the 14th century, however, grain no longer ripened in Iceland. The years between 1314 and 1319 AD were marked by harvest failure in almost every part of mainland Europe. Extremes of weather occurred, with severe winters and unusually hot or wet summers. There are reports of marshes spreading and swollen rivers, reaching a climax in the 15th century. In consequence, the boundaries of cultivation contracted. From estimates of accumulated

temperatures, the cultivated area of the British Isles may have fallen by over two million hectares for climatic reasons between 1300 and 1600 AD (Grove 1988).

Economic and social factors clearly played a major part in the abandonment of arable farming and in the desertion and shrinkage of so many settlements during the late mediaeval period, but successions of cold, wet summers and disastrous harvests, such as those of 1314–16 and 1320–21 AD, may also have had a significant triggering effect. The most frequent reasons given by contemporaries were the decline in village populations, shortage of seed corn, soil exhaustion, and shortage of plough teams (Baker 1966). As Grove (1988) has pointed out, it may also have been relevant that the summers by 1500 AD were already 0.7°C cooler than those of the mediaeval optimum, when the human population had risen relatively rapidly. The growing season may have been three weeks shorter by 1400 AD, and as much as five weeks by the 17th century.

In the decades between the late-16th and late-17th centuries, European glaciers swelled and their tongues advanced, destroying high-level farms and damaging mountain villages. Glacier-fed streams flooded more frequently, sometimes catastrophically. Increased precipitation triggered a greater number of avalanches and landslides. Data from the general tax commissions held in Sunnfjord Fogderi in Norway provide, in the tax relief proceedings, evidence not only of serious damage to farmland in the vicinity of such phenomena, but of a more extensive decline in rural prosperity between 1667 and 1723 AD. Grove and Battagel (1983) attribute this decline to the substantial fall in cattle numbers, which, in turn, was a response to lower temperatures and the shortening of the growing season at that time throughout Scandinavia.

12.3 Effects on the natural habitat

There can be no doubt that these small changes in temperature appear to have had dramatic effects on land use and farming. One effect often referred to is the frequency of vineyards in the *Domesday Book*, describing 11th century England. Vineyards are, however, plentiful in England today and, though the warm summer of 1989 may have increased their production, it is perhaps more a reflection of taste and fashion, or even mediaeval politics, that Bordeaux and Burgundy are more valued now. Certainly, it has not been impossible to grow grapes and make wine in England over the last 50 years when the temperature has been lower than in 1086 AD. Indeed, it was not impossible in the little ice age. Early in the period we find Richard III appointing John Piers master of the vineyard at Windsor. When Henry VIII succeeded to the throne in 1509, there were 139 sizeable vineyards. About 100 years later, William Harrison estimated the production as 630 000 gallons. Samuel Pepys recorded visiting vineyards at Hatfield, Blackheath, and Walthamstow that were producing wine. John Evelyn recorded that the wine of Blackheath was good for little, but Pepys and his companions said of Walthamstow wine: 'they never drank a better'.

As well as vineyards, the *Domesday Book* provides evidence of the distribution of habitats, plants and animals in place names. LEAH, for example, means a woodland glade or clearing, and came into use after 730 AD. The most frequent use is in combination with trees common today, such as oak, ash and thorn, but it also occurs with elm, apple, aspen, birch, and hazel, rather than any species which could be regarded as exotic. There are also grasses in Bentley, ferns in Farnly, heaths in Hoathly and Headly, crows in Crawley and finches in Finchley, none of which sound far-fetched. Bitterns in Purley or wolves in Woolley might not be expected today, but hardly because of a change in climate. Similarly, the absence of deer from Buckworth or Hartay, gadflies from Bawsey, or swans from Iltney are all more likely to have resulted from the direct effect of man's intervention than from changes in climate. None of these place names describe an England which differs from what it could be today (Gelling 1984). Evidence from the trees mentioned in the Anglo-Saxon charters (Rackham 1986) confirms this similarity between the England of the mediaeval warm period and England today. Further confirmation in both trees and herbaceous plants can be found in *Bald's Leechbook*, a herbal written about 900 AD in Winchester. Again, oak, ash, thorn, apple, maple, willow, sallow, elder, hawthorn, dogwood and ivy are mentioned, along with nettles, tansy, betony, knapweed, burdock, groundsel, viper's bugloss, vervain, dittander and corncockle (Crossley-Holland 1984).

About a century later, Aelfric's *Colloquy* gives a simple prose picture of an ordinary England, in a Latin lesson, hunting deer, fishing for pike, eels and trout in rivers, or fishing for herring, salmon, cockles, winkles, crabs, and lobsters at sea.

Unless 'Rough winds do shake the darling buds of May and summer hath all too short a lease of life' is Shakespeare's comment on the little ice age, the poets show that the procession of the seasons was then as it is now, going back through Ausonius 'On new blown roses' to Ovid through the manuscripts of Benedickbeurn. April and May have always been months perceived as we do now.

The historical evidence has to be balanced against other evidence of changes caused by climate. For example, more European migrant birds were recorded in England in the warmer period between 1890 and 1940 than before or since (Williamson 1974). The blackbird (*Turdus metula*) has colonised the Faeroes and overwinters in Iceland. Cetti's warbler (*Cettia cetti*) was a Mediterranean bird around 1900 but from 1920 onward it has moved north and, since 1975, has been nesting in southern England. Equally, the cooler period after 1940 appears to have brought the snowy owl (*Nyctea scandiaca*) to Shetland and the great northern diver (*Gavia immer*) to Scotland. Such changes may be large, but are really significant only

to a minority of enthusiastic bird observers.

The general conclusion from the historical evidence is that a small climatic change may have a considerable impact and could significantly affect man's economic activities, but only cause interesting, minor, variations in the natural world, unless the change continues. An increase in temperature of one or two degrees over the next 50 years is not to be feared, but a continuing increase, for a further 50 years, has no historic parallel.

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